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THE AMERICAN SPECIES OF *TRIUMFETTA* L.[1]

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Introduction

The genus *Triumfetta*, one of the largest of the Tiliaceae, is pantropic in its distribution; the total number of valid species in the genus may approximate 150 or more. Species are especially abundant in Latin America, but extend from tropical Florida through the West Indies, Mexico, and Central America, southward to Argentina.

The western-hemisphere species of the genus have received no special attention from systematists. K. Schumann's[3] treatment of the South American species, though still a standard reference, is however pathetically out of date. Standley's[4] classification of the Mexican species is generally more acceptable, but an array of new species has been established since his publication. About 150 species have been named for this hemisphere, and it was thought desirable to monograph the genus for the New World in order to establish the proper status of the species.

It is realized that the present splitting of the genus with regard to its occurrence in the eastern and western hemispheres, though convenient, is definitely not natural. At least three species which are represented in Latin America are also known to occur in the eastern hemisphere. There is a possibility that other species may have similar distribution. Since this study was undertaken with a view to clarify the species of the western hemisphere, the total range and the remaining species of the genus have of necessity been ignored.

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[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Washington University.

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[3] K. Schumann, in Mart. Fl. Bras. 12^3:131. 1886.

[4] Standley, in Contr. U. S. Nat. Herb. 23^3:741. 1923.

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A large quantity of specimens from nearly all the major herbaria of Europe and of both North and South America has been available for the study. About fifty plants of three species were also grown in a greenhouse, but the living plants were not amenable to such conditions and though they grew steadily none flowered. Hence this study is based entirely on the standard herbarium methods.

In trying to understand the morphology and to clarify the basic species concept in the genus, I realized, as with some previous systematists,[5, 6] that the characters derived from the fruits are easily ascertainable and highly constant for most species. After a primary classification of all the fruiting specimens, an attempt was made to correlate them with the flowering ones. This is rendered imperative, as it is but rarely that one finds both the fruiting and flowering materials on the same specimen. It soon became apparent that certain species are exceedingly distinct in both fruit and flower, while others show considerable variation in the floral characteristics. The species that show the greatest diversity in floral characters are also found to possess extremely polymorphic leaves. To this category belongs the *semitriloba* complex, wherein the greatest number of species have been named.

Mass collections, kindly placed at my disposal by Dr. Edgar Anderson, were studied for two species: *T. semitriloba* and *T. Calderoni*. Though no conclusive proof was arrived at, the study gave sufficient indication that introgression between the species is rampant. The species *T. semitriloba* tends to approach *T. Lappula*, on the one hand, in its characteristic, more or less pandurate leaves and very condensed nodose cymes by the foreshortening of the peduncles and pedicels; and, on the other, *T. bogotensis* by its larger flowers, more showy petals, more densely pubescent fruits, and also by the presence of short simple hairs on the leaves. The variation in the types of inflorescences, and especially the abortion of spines on the surfaces of the fruits (with their presence only on the lateral margins), tend to merge *T. Calderoni* with the genus *Heliocarpus*. Were it not for the presence of the urceolus, certain specimens of *T. Calderoni* would definitely break the generic separation between *Heliocarpus* and *Triumfetta*.

Despite the great quantity of material available for study, at least a third of the species are very imperfectly known; six species being represented only by the types. The genus further presents a problem in distribution, a great many species being strict endemics while a few are pantropic weeds.

A number of species of widespread distribution, as *T. semitriloba*, *T. bogotensis*, *T. Bartramia* and others, apparently have an infinite capacity for variation in minor characters of leaf size, shape, and indument. The extremes often seem quite distinct in themselves but in a study of large numbers of collections they appear to lose their seeming significance. Wherever such intergradations have been found, I have reduced a number of previously described species to synonymy. At the same time I have described a number of novelties which in my opinion are new to

[5] Masters in Oliver, Fl. Trop. Africa 1:254. 1868.
[6] Sprague & Hutchinson, in Jour. Linn. Soc. Bot. 39:231. 1909.

science. With greater abundance of material in the future and intensive study of the genus further reduction may be in order.

History

The genus *Triumfetta* was proposed by Plumier[7] in 1703, in honor of John Baptiste Triumfetti of Bologne, doctor in medicine, lecturer in botany, and director of the botanical garden at Rome. Linneaus[8] in 1737 adopted the genus and described both calyx and corolla, which were depicted in Plumier's rough illustration. In the same year Linneaus[9] gave a detailed description under the same generic name of a plant growing in Clifford's garden, received from either Jamaica or Bermuda, and described it as apetalous. In 1742[10] he altered the description of the genus and stated that it lacked the calyx (corolla). In the first edition of 'Species Plantarum',[11] the description in 'Hortius Cliffortianus' was cited for *T. Lappula*, the only species named under the genus.

Linneaus had already established the genus *Bartramia*[12] which, according to Fawcett and Rendle, was based on a plant in Hermann's Herbarium (now in Herb. Mus. Brit.) with both calyx and corolla. The species *Bartramia indica* was published in 'Species Plantarum' on an earlier page (p. 389) than *Triumfetta Lappula*. As synonyms under *B. indica* Linneaus cited, among others, one of Plukenet's[13] drawings which is rather aptly done and quite diagnostic. Six years later, Linneaus[14] included *Bartramia* in *Triumfetta* and altered the trivial by naming the species *T. Bartramia*.

De Candolle[15], being unable to determine the identity of *T. Bartramia* on the ground that the synonyms cited include many diverse species, adopted Jacquin's name *T. rhomboidea*.[16]. Later botanists followed De Candolle till recently when Fawcett and Rendle[17] established that *T. Bartramia* and *T. rhomboidea* are conspecific. It is, however, to be noted that the earliest trivial is *indica*, but as Lamarck[18] subsequently described *T. indica*, the identity of which is doubtful, it is desirable to adopt the Linnean name *T. Bartramia*. Gaertner[19] maintained the two genera as distinct and further distinguished them by the presence of indivisible fruit with 1-seeded loculi in *Triumfetta*, and divisible fruit and 2-seeded loculi in *Bartramia*. The fruit of *T. Bartramia* is not really dehiscent, but it could be made to separate into component valves by prolonged boiling.

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[7] Nov. Pl. Amer. Gen. 40, *t. 8.* 1703.
[8] Gen. Pl. ed. 1. 344. 1737.
[9] Hort. Cliff. 210. 1737.
[10] Gen. Pl. ed. 2. 243. 1742.
[11] Sp. Pl. ed. 1. 444. 1753.
[12] Fl. Zeylanica, 77. 1748.
[13] Almagest. Bot. 206, *t. 41, f. 5.* 1691.
[14] Syst. Pl. ed. 10. 1044. 1759.
[15] Prod. 1:508. 1824.
[16] Enum. Pl. Carib. 22. 1760.
[17] Jour. Bot. 59:224. 1921.
[18] Encyc. Meth. 3:420. 1789.
[19] Fruct. & Sem. 2:137. 1791.

De Candolle[20] finally united the two genera and established two sections Bartramia and Lappula based on Gaertner's diagnosis, where Lappula is separated from Bartramia by the lack of petals and by its indivisible fruits. Endlicher[21] adopted the sections of De Candolle but defined them entirely on the fruit characters. Baillon[22] substituted the name Eutriumfetta for Lappula and still distinguished it from Bartramia by the indehiscent fruit. K. Schumann[23] was dissatisfied with the classification based entirely on the characters of the fruit. To him the fruits (and also the leaves) were extremely polymorphic and did not offer any constant characters. He redefined the sections, basing his classification entirely on floral characters: Eutriumfetta being apetalous and without a glandular gonophore, and Bartramia with manifest petals and glandular gonophore.

Sprague and Hutchinson[24] disagreed with K. Schumann's classification as it separated the two very closely related species *T. semitriloba* and *T. Lappula*. They in turn proposed a new classification based on a study of fruits, inflorescences and certain characters derived from the indument of the sepals. According to them, the genus is divided into the following four sections:

1. Lepidocalyx: Calyx scaly without; stamens numerous (25–60); ovary 10-loculate, each cell with 1 ovule; fruit spheroid, woody, 8- to 10-loculate, each 1-seeded, the spines fusiform.
2. Propa: Calyx not scaly; stamens numerous (25–40); ovary 6- to 10-loculate, each with 1 ovule; fruit spheroid, woody, 6- to 10-loculate, each 1-seeded, the spines constricted at the base and the tip.
3. Lasiothrix: Calyx not scaly; stamens usually numerous (20–50), rarely few; fruit spheroid, not woody, very light, indehiscent, often 1-seeded, the spines weak, with plumose tip.
4. Lappula: Calyx not scaly; stamens numerous or few; fruit spheroid or ovoid, dehiscent or indehiscent, many- or 1-seeded, the spines rigid, the tips rarely plumose.

Since the above classification, there has been no appreciable study of the genus as a whole. Hochreutiner's[25] work is more in the nature of reorganization of the tribe Grewieae than of the genus itself.

Geography

Triumfetta is pantropic in its distribution. There are 43 species in the western hemisphere, about 50 in Africa and 10 in Australia. The number of valid species in Asia is not known, but may approximate 40 or more. *T. Bartramia* and *T. Lappula* are equally at home in both the eastern and western hemispheres. *T. semitriloba* is abundantly represented in the western hemisphere and to a lesser

[20] Loc. cit. 506. 1824.
[21] Gen. Pl. 1008. 1840.
[22] Hist. Pl. 4:195. 1873.
[23] Mart. Fl. Bras. 12^3:131. 1886.
[24] Jour. Linn. Soc. Bot. 39:233. 1909.
[25] Ann. Conserv. Jard. Bot. Genève 18:92. 1914.

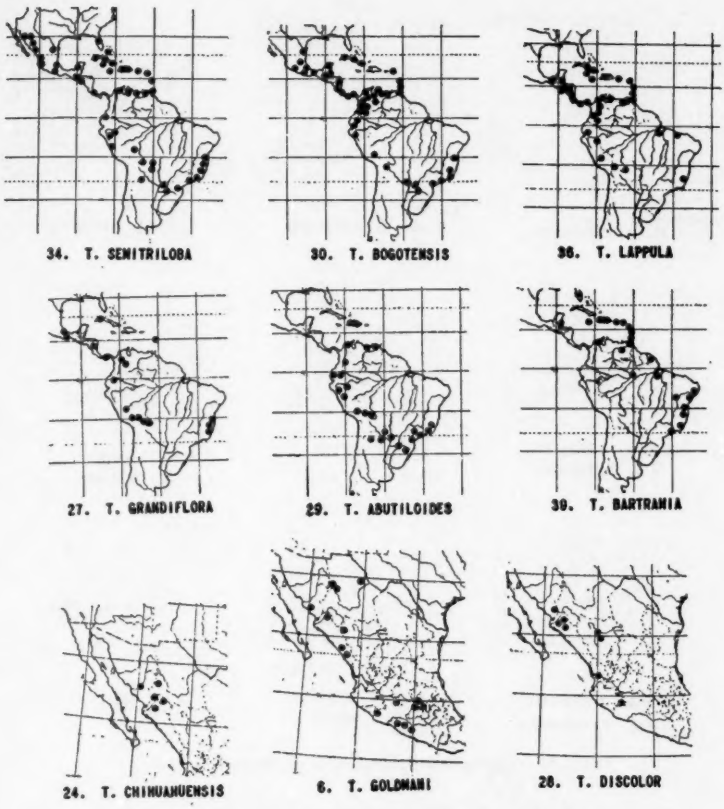

Fig. 1. Geographical distribution of species of *Triumfetta*.

extent in Africa and eastern and southeastern Asia. In the western hemisphere the species extend from tropical Florida to the West Indies, Mexico, and Central America southward to northern Argentina. Species are especially abundant in Mexico and Central America.

There are six species with very extended ranges found in both North and South Americas. The three very closely related species, *T. bogotensis*, *T. semitriloba*, and *T. Lappula*, have very similar ranges, each extending from Mexico and the West Indies through Central America southward to northwestern South America, finally to central and eastern South America. *T. grandiflora*, one of the more primitive species, has similar north-south distribution, but is rather sparsely represented throughout its range. *T. Bartramia*, whose affinities with the western-hemisphere species is rather doubtful, has an altogether distinct distribution. It

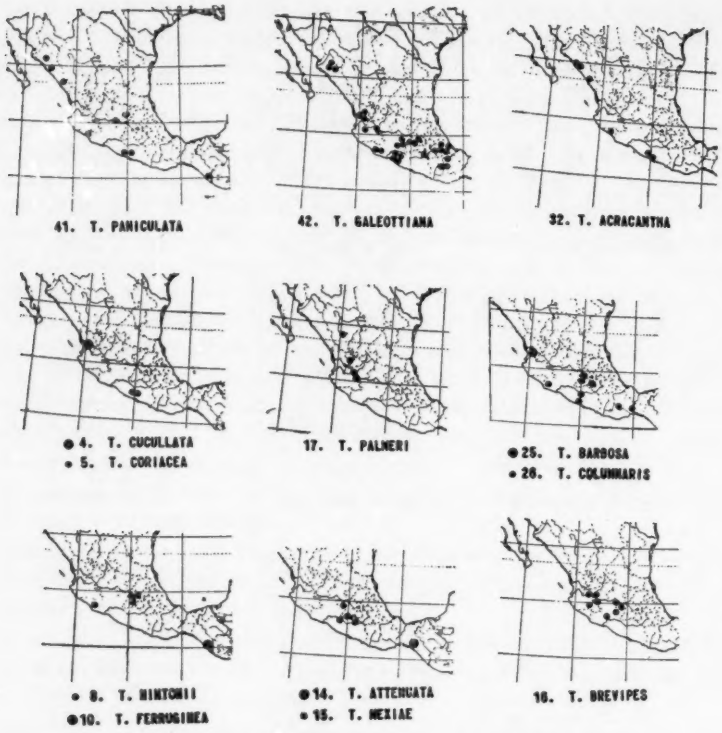

Fig. 2. Geographical distribution of species of *Triumfetta*.

is known in the West Indies and eastern South America, and except for one locality in British Honduras and in Florida, where introduced, it is not represented on continental North America. *T. abutiloides* approximates the distribution of its closely allied species *T. bogotensis*, except that it is not known in continental North America.

There are nine species known only from South America. *T. althaeoides*, which frequents lowland sandy areas, is austral in its distribution, and is found extensively in northern South America wherever suitable habitat is available. *T. obscura*, which is the counterpart of *T. acracantha* from Mexico, is confined to southeastern Brazil. *T. Sampaioi*, a species closely related to *T. Bartramia*, is known only in the lowlands of northeastern Brazil. The three closely related species, *T. longicoma*, *T. multilocularis*, and *T. mollissima*, are found exclusively in southeastern Brazil, Peru, and Colombia respectively. *T. caudata*, *T. sericata*, and *T. persimilis* occupy narrow ranges in Colombia.

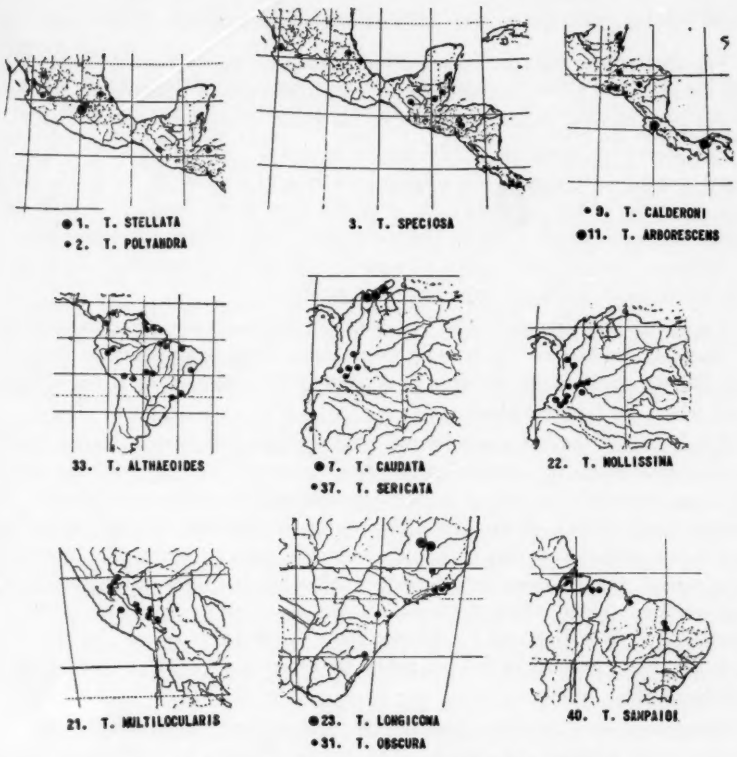

Fig. 3. Geographical distribution of species of *Triumfetta*.

The majority of the species are found in Mexico, and among them are a few that extend into Central America. The two more primitive species, *T. polyandra* and *T. speciosa*, though found sparsely in any particular locality, extend southward into Central America. Most of the species are known only from central and western Mexico. *T. discolor*, *T. Goldmani*, *T. acracantha*, *T. paniculata*, and *T. Galeottiana* are the most prominent species of western Mexico, while *T. brevipes*, *T. Palmeri*, and *T. columnaris* are found rather abundantly in central and southwestern Mexico. The rest of the species are endemics, being known from very restricted areas.

The series GENICULATAE is best represented in Mexico and Central America. Of its fifteen species only two (*T. caudata* and *T. persimilis*) are from Colombia. Because of the presence of the majority of species in central Mexico and northern Central America, including most of the primitive ones and also many very restricted endemics, it is assumed that the primary centre of dispersal of the species is probably from that area.

MORPHOLOGY

The species of *Triumfetta* are a diverse group of woody plants, usually small trees or shrubs. The series GENICULATAE constitutes species wherein the tree habit is most predominant, although no tree in the genus is known to exceed 5 m.

The stems are terete in all the species except *T. paniculata* where they are ridged or irregularly angled, the ridging occurring as a result of decurrent petiole bases. Certain plants, especially those in the *semitriloba* complex, have a short branch at almost every node of the main axes, while others (as represented by *T. Calderoni*) are sparsely, if ever, branched. The bark is prominently lenticellate, with either small white or large brown lenticels.

The leaves are petiolate. The length of the petiole is usually correlated with the shape of the lamina, the broadly ovate leaves being long-petiolate while the large elliptic ones are shortly so. *T. obscura* is an exception as it has elliptical leaves which are long-petiolate.

The lobing of the leaf generally is a good primary character in certain species, but in others, such as *T. semitriloba*, *T. bogotensis*, and *T. Bartramia*, the general leaf-shape is so variable that it is relatively useless as a definitive character. In general, weedy species of the genus have variously indented or lobed leaves and show much greater variation than the non-weedy ones. The margin is serrated, the serrations usually being very irregular. Most species have small glands on the basal serrations from which the mucilaginous sap exudes. In three species, *T. althaeoides*, *T. cucullata*, and *T. coriacea*, these glands are found on the petioles at the basal sinus. Because of their extreme constancy they offer an easy means of identifying these species.

The term "bract" has been used in this paper to mean the terminal leaves of a branch which subtend the cymes. The bracts are usually very prominent in plants with axillary inflorescences. They are invariably smaller and more shortly petioled than the vegetative leaves and are generally elliptical in outline. No measurements of the bracts are given, as it is difficult to determine from dried material whether they have attained their maximum growth or not.

All species have more or less coarsely pubescent leaves, except *T. acracantha* and *T. obscura* which have glabrescent ones. The leaves usually possess three tiers of induments, two of which consist of stellate hairs, one closely appressed to the surface and the other usually much larger and spreading irregularly, the third tier of simple hairs which are usually much longer and generally more prominent. The nature of the indument offers good primary characters in certain species. However, the use of this character requires great judgment as the pubescence changes considerably during the course of development. Young leaves may be covered rather densely with both stellate and simple hairs, while the mature ones on the same plant may have hairs of one kind only.

The leaves are stipulate. The stipules are usually large and linear and tend to dry from the tip to the base. They are rarely caducous; in most species they

persist even after the shedding of the leaves. No diagnostic importance has been attached to the stipules.

The inflorescence consists of compound aggregate dichasia. In the more primitive species, the cymes, each consisting of 1–3 cymules, are borne in the axils of the bracts. In the more advanced species the cymes are terminal and consist of a shortened sympodial branch system, each bearing 4–6 cymules. There is usually more than one cyme per bract, the cymes being clustered rather densely at the nodes, and the whole inflorescence is usually large and spreading. In both types of inflorescences the cymule is either 2- or 3-flowered. Each cymule is subtended by a pair of fugacious bracteoles. The number of flowers per cymule is not constant even on the same inflorescence, probably due to the abortion of one of the lateral flowers in early ontogeny. The inflorescences are hermaphrodite or, in a few species, gynodioecious.

The species of the genus have considerable range in the size of flowers. Slightly before anthesis the floral buds of *T. polyandra* and *T. speciosa* are as large as 3–4 cm. in length, while those of *T. Lappula* and *T. heliocarpoides* rarely, if ever, exceed 6 mm. The size of the flower is generally a good constant character for most species. However, in *T. bogotensis* the length varies from 7 to 13 mm. and is not correlated with the variations in either the fruit or vegetative characters.

The floral buds in the majority of the species are oblongoid, but in the *Galeottiana* and *Calderoni* complexes they are obovoid in the hermaphrodite flowers.

The sepals afford good specific characters. All plants of the genus bear a subapical appendage on the sepals, the lengths of which are generally constant for a given species. *T. Purpusii* and *T. falcifera* possess the longest appendages, usually about 5 to 7 mm. long, and *T. Calderoni* the shortest, being nearly obsolete. Unless otherwise mentioned, the lengths of the sepals given in this paper include the apical appendages. The indument of the sepals may also be used as a primary character in certain species. However, as with the pubescence of the leaves, its use in the identification of a species needs caution.

There is a tendency in the genus towards a completely apetalous condition. The more primitive species, such as *T. polyandra, T. multilocularis, T. brevipes* and others, have large showy petals, while the more advanced species *(T. Lappula, T. Galeottiana,* and *T. heliocarpoides)* are either apetalous or possess very small ones. The petals have a short ciliate claw, which is hairy on the outside and sometimes has a transverse band of stellate hairs on the inner surface at the base of the blade.

The androgynophore or gonophore, with its five spherical or elliptical glands, contributes some important diagnostic characters. The shape of the glands, their size, and whether they are contiguous or otherwise, are usually constant for a species. Because of their extreme smallness, these characters, though mentioned in the specific descriptions, have not been used in the key. The gonophore is slightly accrescent in fruit. *T. Lappula* is the only species known which does not possess a glandular gonophore.

The urceolus is a small, rather membranaceous ring with a ciliate margin, which is borne on the gynophore and completely surrounds the base of the stamens. It is usually 5-lobed sometimes 10-lobed, and very rarely unlobed. *T. Lappula* and *T. Sampaioi* do . . possess an urceolus.

The stamens are borne cyclically on the gonophore, and the number is of great importance in specific criteria. Certain species have as high as 60 *(T. attenuata, T. arborescens)*, others have about 40 *(T. polyandra, T. Purpusii, T. paniculata)*, while the majority of the species possess between 15 and 25. *T. Sampaioi* is the only species in the western hemisphere which has only 5 stamens. The smaller numbers are rather rare in *Triumfetta*. At least three species are known to be gynodioecious. In these the pistillate flower either has staminodes or lacks them completely. No staminate flower is known for the whole genus.

The filaments have retrorse serrations in both the *semitriloba* and *Bartramia* complexes. Other species have smooth filaments. In *T. chihuahuensis* the bases of the filaments are lightly stellate-pubescent. The anthers do not yield any character of diagnostic value. They are always dorsi-fixed, consisting of two thecae, each with two introrse, longitudinally dehiscing cells. The pollen grains are ellipsoidal, and about 50 μ long and 35 μ wide. The surface is minutely rugulose to very nearly smooth.

The number of cells of the ovary is a good specific character. In the series GENICULATAE, the ovary is invariably 2-merous, and in most species of UNCINATAE it is 3-, and rarely 2-loculate. Where the ovary is too small for convenient dissection, the number of locules may be ascertained by dissecting a very small floral bud, and counting the number of stigma lobes. In more mature buds the stigmas, in most species, fuse and do not separate easily. In certain species, however, the stigmas remain separate throughout. The descriptions of the stigma under each species in this paper is that of the later stage.

The style is usually much longer than the stamens, and the stigma is generally exserted above the anthers. However in *T. dioica* and the species of the *Galeottiana* complex the style is shorter than the stamens and the stigma is included by the anthers. It may be of interest to note that these species are the only ones known in the genus which exhibit gynodioecism.

The spinules are small transparent epidermal outgrowths of the ovaries. They are the first to differentiate on the ovaries and retain their shape and size on the mature fruits. They are probably secretory in function, as there are large quantities of mucilage in the early stages of ovary differentiation. In the series STELLATAE and GENICULATAE these spinules are always straight-pointed, while in UNCINATAE they are arcuately recurved. After fertilization, the spines develop from the pericarp, each at the base of a spinule. Sometimes, as in *T. caudata* and especially in *T. Hintonii*, spines fail to develop from every spinule. The spinules are thus carried at the tips of the spines, and usually harden slightly after anthesis. Whatever their degree of rigidity, the spinules are always transparent and hyaline. The nature of the spinules on young fruits, slightly after fertilization, is the best

criterion for determining to which series the plant belongs.

The fruit is the best single character for determining the species. The shape is generally constant for a species. *T. caudata*, *T. Hintonii*, and *T. socorrensis* possess oblongoid fruits, while the rest of the species have either spheroid or suborbicular ones. It may be noted that these three species possess much fewer spines than the others.

It is often difficult to speak with certainty regarding the dehiscence of the fruits. In at least three species (*T. polyandra*, *T. grandiflora*, and *T. discolor*) the fruits are easily dehiscent. In certain others, such as *T. semitriloba*, *T. multilocularis*, and *T. althaeoides*, they are quite indehiscent. In a few the fruit can be made to separate into valves by prolonged boiling, but there is no evidence that it actually dehisces in nature.

The number of cells is constant for a given species. Each cell is potentially 2-seeded, but there is a general tendency in most species to the formation of false septae and production of double the number of cells in mature fruit, each with one seed. The reverse is true in three species, *T. Hintonii*, *T. Bartramia*, and *T. Lappula*, where one or more cells abort early in the process of fruit development.

The size of the mature fruit body shows little variation. However, care is needed in the use of this character, as it often is difficult to know from dried material whether a fruit is mature. In general, species with large showy flowers tend to have relatively large fruits. *T. althaeoides* and *T. paniculata* are obvious exceptions as they possess rather large fruits but have very small flowers.

The nature of the pubescence on the fruit is less variable than that of the leaves and stems. Certain species, such as *T. Mexiae* and those in the *Galeottiana* complex, possess glabrous fruits. Sometimes two rather closely allied species may be essentially different only in the pubescence of the fruit body (*T. Purpusii* and *T. falcifera*). In *T. Lappula* a few fruits have been noticed to have densely pubescent bodies and long plumose hairs on the spines when either diseased or attacked by insects. This may be interpreted as traumatic reversion to an ancestral character.

While the general nature of the spinules affords characters for series, those of the spines themselves are characteristic of individual species. The spines may be glabrous or pubescent. When pubescent, they may bear many long hairs (plumose) or short rather irregularly arranged hairs (irregularly pubescent) or short hairs which are all retrorsely pointed (retrorsely pilosulose). Further, the length of the spines and the number per fruit being reasonably constant for a given species, they have been found satisfactory in primary separation of the species. Section LAPPULA is characterized by rigid spines; the only known American species with more or less flexible spines is *T. longicoma*.

The seeds are either ovoid or lenticular, and have a prominent funicular groove. There is a considerable variation in the size of the seeds among the species. Measurements of the mature seeds are given under every specific description.

Generic and Subgeneric Relationships

Triumfetta is commonly referred[26] to the tribe Grewieae of the family Tiliaceae and usually is recognized by its characteristic bur-like fruits. The genus is distinct from the other genera of Grewieae except *Heliocarpus*. Some of the more important distinguishing characters between the two genera have been enumerated in my revision of the genus *Heliocarpus*.[27]

In their treatment of the African species of *Triumfetta* Sprague and Hutchinson[28] divide the genus into four sections based on the texture of the fruits, the nature of the spines and the inflorescences, and some characters derived from the indument of the sepals. According to their classification all the American species belong to section Lappula, under which they tentatively proposed the three series Stellatae, Geniculatae and Uncinatae.

Before considering the series in detail it is desirable to summarize here the characters of the genus which have been considered primitive:

1. Arborescent habit as opposed to shrubs or annuals.

2. Dense tomentum of both stellate and simple hairs on leaves and branches, usually associated with plumose hairs on spines *versus* glabrescent condition of leaves and branches together with glabrate or retrorsely pilusolose spines.

3. Simple inflorescences consisting of 1 or 2 cymules in the axils of the bracts as compared with compound aggregate dichasia where the cymes are borne in dense nodose clusters of 12–20 flowers each.

4. Large showy flowers with many stamens, and multiloculate large fruits *versus* small flowers having few stamens with a tendency towards dioecism; also marked tendency towards reduction of floral parts such as gonophore, gland, urceolus, and petals, and the general progress towards 1-loculate, small, glabrous fruits.

The series Stellatae is known to me from only one specimen, and I am in no position to comment on its phylogeny or relative antiquity, except to say that it is very closely related to Geniculatae. The spinules on the ovary are straight and undivided and resemble those in Geniculatae; but in fruit they consist of 4 to 5 per spine and are stellately arranged.

The series Geniculatae is a relatively small group consisting of 14 species, most of which are rather poorly represented in the herbarium. The species of this series generally possess a tree habit, 2-merous ovary, usually numerous stamens, and ovaries bearing spinules which are either straight or slightly deflexed in fruit, but never recurved. Each spine is terminated by one spinule only. These characters, together with the obvious consideration that a hooked spinule of Uncinatae is definitely more efficient in the dispersal of fruits than the straight one of Geniculatae, lead one to the conclusion that Geniculatae is more primitive.

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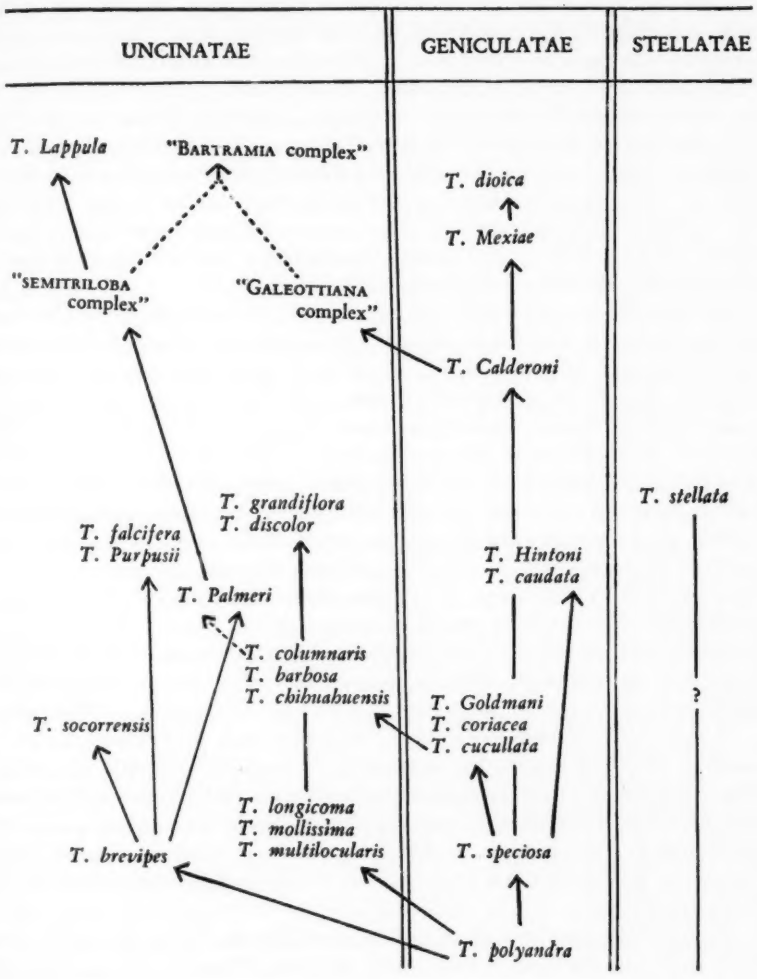
[26] K. Schumann in Engl. & Prantl, Nat. Pflanzenfam. 3[6]:28. 1895.
[27] Ann. Mo. Bot. Gard. 36:508. 1949.
[28] Jour. Linn. Soc. Bot. 39:233. 1909.



Triumfetta polyandra is apparently the most primitive species of the series since it possesses very large showy flowers (the largest known for the genus), numerous stamens, and also very large fruits with very densely plumose spines. The character of the spines in turn relates it to LASIOTHRIX, a section considered to be more primitive than LAPPULA by Sprague and Hutchinson.

The derivation of the species of GENICULATAE from *T. polyandra* is apparently quite simple. *T. speciosa,* with its very large flowers and fruits and its long plumose spines, could be derived from *T. polyandra,* from which it differs in having fewer stamens and much smaller petals. By the reduction in the sizes of flowers and fruits and also in the number of spines, *T. caudata* could be conveniently arrived at from *T. speciosa. T. caudata* possesses very plumose spines and densely tomentose fruits, leaves, and branches. *T. Hintonii* culminates this line of reduction, as it has glabrescent leaves and branches, much smaller flowers, very few short spines, and a 1-loculate ovary due to the abortion of one locule. In *T. caudata,* and especially in *T. Hintonii,* the number of spines per fruit is usually much less than the number of spinules on the ovary.

Another line of evolution which stems from *T. speciosa* leads to the *Calderoni* complex, consisting of seven species. The more primitive species of this complex are characterized by the possession of plumose spines and small but densely tomentose fruit bodies. They all have very small flowers usually borne on compound aggregate dichasia, in which each cyme is composed of 12–20 flowers. The derivation of the flowers of this complex from *T. speciosa* is not too clear. The three species, *T. Calderoni, T. ferruginea,* and *T. arborescens,* are considered more primitive than the rest of the species in the complex, since they possess numerous stamens, plumose spines, and densely tomentose fruits. *T. Mexiae* is the only species of the genus which has a small gynophore borne upon the gonophore. This character, in conjunction with the glabrate fruits and spines and fewer stamens as compared with the three species mentioned above, makes *T. Mexiae* appear definitely more advanced. *T. attenuata* is very closely related to *T. Mexiae.* Dioecism is attained in *T. dioica,* a species which shows close affinity with *T. Calderoni.*

A second line of evolution from *T. polyandra* leads to *T. coriacea* and *T. cucullata.* It is unfortunate that no fruiting specimen of *T. cucullata* is available. However, in its vegetative and floral characters it is strikingly similar to *T. coriacea,* a species which has numerous stamens and large flowers with showy petals. It differs from *T. polyandra* in its smaller fruits and fewer and less pubescent spines. Except that *T. Goldmani* has fewer stamens, it has much the same characters as *T. coriacea.*

The series UNCINATAE is rather well represented in the herbarium and consists of 27 species in the western hemisphere and about 25 in the eastern. Unlike GENICULATAE, this series is not a compact group, and is apparently polyphyletic in origin, as some of the species with uncinate spinules could be derived more easily from species in GENICULATAE than from those in UNCINATAE. This series is characterized by the members having spinules which are continuously recurved both on the ovary and the spine, by their shrubby habit, by the predominance of 3-merous ovaries, and, except in the more primitive species, by the presence of only 5–25 stamens.

The most obvious direct line of evolution is from *T. brevipes* which, though advanced in many respects, could be easily referred to *T. polyandra* on such primitive characters as the size of the flowers, the presence of numerous stamens, and the large, more or less tomentose fruits with numerous though short spines. This species apparently gives rise to three lines of evolution, of which two end in strict endemism and the third attains a high degree of success and complexity.

In possessing relatively large, showy flowers, and large, more or less tomentose fruits and spines, the endemic species *T. socorrensis* is obviously related to *T. brevipes*; however, it is more advanced than the latter as the number of spines and stamens is considerably less. *T. Purpusii*, another endemic species, has the same type of fruits as *T. brevipes*, though they are slightly smaller and armed with fewer spines. Its flowers still possess numerous stamens, but are rather oddly specialized in having excessively long apical appendages of the sepals. The relationship between *T. Purpusii* and *T. falcifera* is so close that it is sometimes slightly difficult to distinguish the two species when in flower. The fruits of *T. falcifera* and *T. Purpusii* are alike in general shape and size but those of the former are nearly glabrous.

The more successful line of evolution from *T. brevipes* leads to *T. Palmeri*. An interesting specialization appears here for the first time. The spines are clothed lightly with short hairs which are all retrorsely pointed. This feature, together with hooked spinules, is of definite advantage in the dispersal of the fruits by animals. Though *T. Palmeri* has retrorsely pilosulose spines, it still possesses large flowers and fruits. The highly successful and widely distributed *semitriloba* complex may be derived from this type by the reduction in the sizes of flowers and fruits, and also by the inflorescences becoming slightly more compound. Further reductions in the floral parts leads to *T. Lappula*, a very widely distributed species of the genus.

There is a considerable confusion with regard to the delimitation of *T. semitriloba*. Some authors[29, 30] treat it in a very inclusive sense, to include all plants which have retrorse hairs on their spines but are not *T. Lappula*. This inclusive interpretation is not satisfactory, because some of the segregate species are distinct even to a casual observer.

It is more usual to split the complex into many species, chiefly distinguishing them on the size of the flowers, shape and size of the leaves, and on pubescence. This treatment does not solve the problem either, as most of the so-called species appear to be connected by numerous intermediate forms which defy classification in the herbarium. The difficulty is further enhanced by the incomplete nature of the specimens, classification being frequently uncertain in the absence of mature fruit.

The variation in the size and shape of the leaves is of such great magnitude that it is usually impossible to match two specimens with any degree of certainty by

[29] K. Schumann in Mart. Fl. Bras. 12^3:135. 1886.
[30] Uittien in Pulle, Fl. Surinam 3:56. 1932.

the use of leaf characters only. Other characters being very similar, the leaves usually may vary from undivided to deeply and profoundly 3-lobed, the lobing being either above or below the middle of the lamina. The size of the flowers is relatively less variable, but there are instances, especially in *T. bogotensis*, where it does not correlate with the other trends. The nature of the pubescence is slightly more constant, though there is a very considerable variation in the degree. Apparently the kind of hairs, whether stellate, simple, or both, is generally constant for a species, as it tends to vary with the general shape and size of the petals and fruits together with the number of locules and the nature of the spines.

On some of these more constant characters, I have recognized six species in the *semitriloba* complex, with the hope that it would be more satisfactory from both the practical and taxonomic standpoints. Some of the more important characters which help in the identification of the species are discussed briefly under each, besides those mentioned in the key.

The three South American species, *T. multilocularis*, *T. mollissima*, and *T. longicoma*, are related in but a superficial way to *T. brevipes*. The very definitely 2-merous ovaries, the general tendency towards a tree habit, and the large fruits with very plumose spines relate them more closely with *T. polyandra*. Among themselves, the relationships to one another are extremely strong. *T. multilocularis*, though a very distinct species, has hitherto been mistaken for *T. mollissima* in the herbarium. *T. longicoma* is the most advanced member of the three.

Triumfetta chihuahuensis, *T. barbosa*, and *T. columnaris* are three distinct but very closely related species. Although they have a few characters in common with *T. Palmeri*, they do not exhibit any close affinity to that species and are much more closely related to *T. coriacea* and *T. Goldmani*. Without the uncinate spinule, one would certainly experience difficulty in identifying *T. columnaris* and *T. Goldmani*. It is most probable that these three species of UNCINATAE are derived directly from the three geniculate species, *T. cucullata*, *T. coriacea*, and *T. Goldmani*. *T. grandiflora* and *T. discolor* are definitely related in having dehiscent fruits and rather large showy flowers with about 20 stamens. They are in turn related to *T. mollissima*.

The *Galeottiana* complex (consisting of the three species, *T. paniculata*, *T. Galeottiana*, and *T. heliocarpoides*) is of great interest in that though the three are definitely uncinate, they do not show any close affinity with any other species of the series. However, there is a very remarkable similarity between this complex and the *Calderoni* complex in GENICULATAE. The two complexes have the same type of inflorescence, flowers of the same shape and structure, and fruits whose superficial resemblance is rather striking despite the fact that all species of the *Galeottiana* complex have essentially glabrous fruits. All species in the *Calderoni* complex have 2-merous ovaries, and *T. paniculata* bridges this difference in possessing a 4-loculate fruit. The affinity is further strengthened by the

tendency of *T. paniculata* to a tree habit, its numerous stamens, and its relatively large fruit. *T. Galeottiana* and *T. heliocarpoides* are not only closely related species but are also very closely allied with *T. paniculata*. Though the three are distinct, sometimes the delimitation of the species becomes very difficult especially when immature fruiting specimens are being considered. Both *T. Galeottiana* and *T. heliocarpoides* attain gynodioecism.

The *Bartramia* complex, consisting of four species, *T. sericata*, *T. brachistacantha*, *T. Bartramia*, and *T. Sampaioi*, is really problematic in its relationships. In the possession of cymes in dense nodose clusters the species resemble those of the *Galeottiana* complex, but, on the other hand, the oblongoid floral buds and pubescent fruits make them resemble the *semitriloba* complex. The picture is further complicated by the fact that *T. Bartramia* is a pantropic weed which is equally at home in both the eastern and western hemispheres. Though the complex does not attain gynodioecism, there is considerable reduction in the floral parts and in the size of the fruits, which are the smallest known for the American species. The fact that *T. Sampaioi* lacks an urceolus and has only five stamens places it in approximately the same degree of advancement and specialization as *T. Lappula*. *T. sericata* resembles *T. bogotensis* in having the same general type of flowers and indument, but has much smaller fruits with glabrous spines. *T. brachistacantha* has characters which are about intermediate between those of *T. sericata* and *T. Bartramia*. The relationships of the species of the *Bartramia* complex with those of the western hemisphere are not too apparent. Its affinity may be with either the *semitriloba* or *Galeottiana* complexes, or possibly with both.

From the above discussion of some of the salient characters and relationships of the species, it is quite obvious that no definition of the series could be given which would suit all the species. The characters are superposed in such a manner that hardly any two are correlated. I am unable to give any precise definition of the series as there are nearly as many exceptional forms as there are typical ones. Further, an attempt at classifying the genus based on characters derived from the size of the flowers, types of inflorescences or the nature of the stigmas (as suggested by Hochreutiner[31]) leads one into similar dilemmas.

Because of these apparent reticulate combinations of the characters, I am led to the conclusion with the original authors that the "series, though very useful for the purposes of a *clavis*, do not coincide with natural groups, but appear to represent three of the phylogenetic stages through which many species of section LAPPULA have passed, the stellate arrangement being the most primitive and the uncinate the most highly modified."[32] The three series are here maintained not only for the sake of convenience, but because they are the nearest approach to the real relationship of the species.

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[31] Ann. Conserv. Jard. Bot. Genève 18:92. 1914.
[32] Sprague & Hutch. Jour. Linn. Soc. Bot. 39:240. 1909.

CHROMOSOME COUNTS

Chromosome counts were made for the following three species:

Triumfetta Bartramia 2n 32
Triumfetta Calderoni 2n 32
Triumfetta semitriloba 2n 32

The counts were made from root-tips of plants raised in a greenhouse at Missouri Botanical Garden. The seeds for *T. Calderoni* were collected by Dr. Edgar Anderson from Honduras, and those for *T. Bartramia* and *T. semitriloba* were sent to me by Dr. Brandao-Joly from São Paulo, Brazil. As none of the plants flowered meiotic counts could not be made.

ACKNOWLEDGMENTS

I have been able to examine specimens, including many valuable types, from several major herbaria in Europe and North America and South America. The herbaria where specimens have been obtained for study, together with the symbols[33] employed in their citations are as follows:

BR Jardin Botanique de l'État Bruxelles.
C Universitetes Botaniske Museum, Copenhagen.
FM Chicago Natural History Museum, Chicago.
G Institut de Botanique Systematique de l'Université, Genève.
GH Gray Herbarium of Harvard University, Cambridge, Mass.
K Herbarium Royal Botanical Gardens, Kew.
MICH University of Michigan Herbarium, Ann Arbor.
Mo Herbarium Missouri Botanical Garden, St. Louis.
NY Herbarium New York Botanical Garden, New York.
P Muséum National d'Histoire Naturelle, Paris.
R Museu Nacional, Rio de Janeiro.
S Naturhistoriska Riksmuseet, Stockholm.
TRIN Herbarium Department of Agriculture, Port of Spain, Trinidad.
U Botanisch Museum en Herbarium, Utrecht.
UC University of California Herbarium, Berkeley.
US U. S. National Herbarium of Smithsonian Institution, Washington, D. C.

Dot maps have been prepared from most of the specimens from which the exact locality could be determined. In the Index to Exsiccatae all the numbered and most of the unnumbered collections have been cited.

I wish to acknowledge my indebtedness to the curators of the institutions mentioned above, and to the Director of Missouri Botanical Garden, where this study was made. For illustrations and aid in chromosome counts I am indebted to Marilyn Amy Gage. Particular thanks are due to Dr. R. E. Woodson, Jr., for his advice, guidance, and constructive criticism.

TAXONOMY

TRIUMFETTA L. Sp. Pl. ed. 1. 444. 1753; DC. Prod. 1:506. 1824; K. Schum. in Mart. Fl. Bras. 12^3:131. 1886, in Engl. & Prantl, Nat. Pflanzenfam. 3^6:28. 1895; Sprague & Hutch. in Jour. Linn. Soc. Bot. 39:231. 1909; Hochr. in Ann. Conserv. Jard. Bot. Genève 18:92. 1914.

Bartramia L. Sp. Pl. ed. 1. 389. 1753.

[33] The symbols used are as suggested by Lanjouw in Chron. Bot. 5:143. 1939.

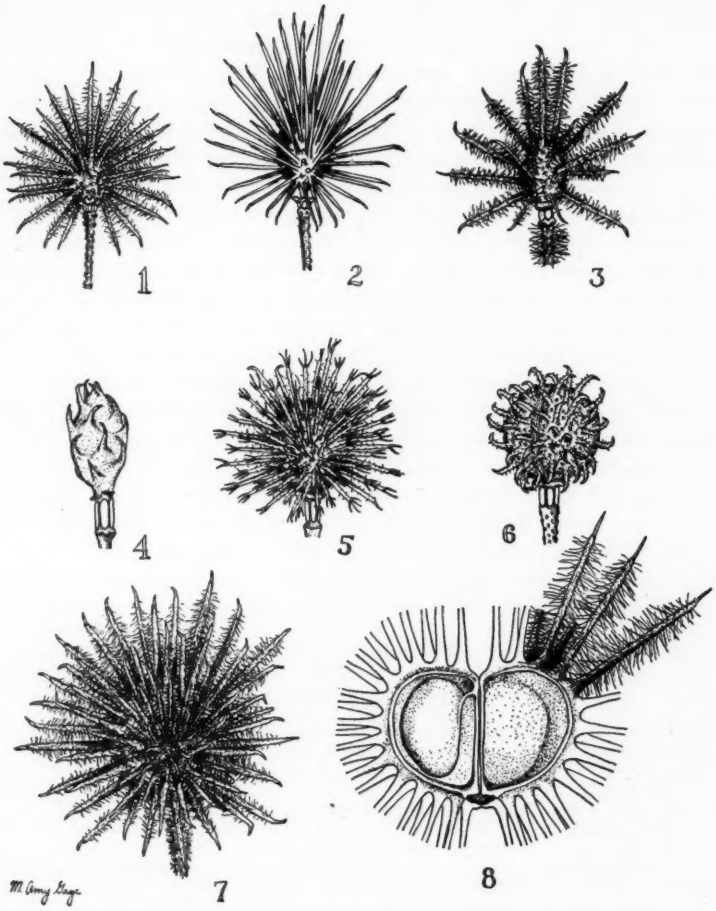

Fig. 4. Illustrations of taxonomic criteria for Series STELLATAE and GENICULATAE:

1. Small orbicular fruit of *T. Calderoni* with densely plumose spines.
2. Suborbicular fruit of *T. Mexiae* borne on a short gynophore above the gonophore.
3. Suborbicular to oblongoid fruit of *T. caudata* with about 25 plumose spines.
4. Oblongoid fruit of *T. Hintonii* with few short spines.
5. Fruit of *T. stellata* with 3–5 spinules per spine.
6. Orbicular fruit of *T. Goldmani* with falcate spines.
7. Large fruit of *T. speciosa* with densely plumose spines.
8. Large, easily dehiscent fruit of *T. polyandra* with large, very densely plumose spines.

Shrubs or trees. Leaves alternate, petiolate, stipulate, the stipules usually large, persistent, rarely fugacious, the blade 3- to 5-lobed or undivided, the venation palmate, 5- to 7-costate at the base. Inflorescences hermaphrodite or gynodioecious, usually axillary, (terminal in few species), consisting of numerous aggregate dichasia. Flowers either hermaphrodite or pistillate, staminate ones not known, hypogynous, 5-merous; sepals 5, valvate, free, with apical appendages; petals 5, sometimes absent, free, imbricate, 3- to 5-nerved, shorter than the sepals, usually ciliate at the base (claw); gonophore bearing 5 spherical or elongate glands manifest, absent in some species, usually crowned by a ciliate, rather membranaceous ring (urceolus) surrounding the stamens; stamens 5–60 in hermaphrodite flowers, staminodial or absent in the pistillate, borne cyclically on the enlarged gonophore, with 2 thecous, 4-celled, introrse, longitudinally dehiscent anthers, the filaments free, usually glabrous, sometimes pubescent at the base, often with retrorse serrations; ovary wholly superior, sessile on the gonophore (except in *T. Mexiae*, with very short gynophore on the gonophore), ellipsoid to orbicular, covered with many short, either erect or recurved, hyaline spinules, 2- or 3-loculate, each with 2 anatropous collateral pendulous ovules, the style filiform, the stigma briefly 2- or 3-parted, sometimes capitate. Fruits dry, indehiscent or loculicidally dehiscent, 2- or 3-loculate, each cell 2-seeded, or falsely 6- to 9-loculate, or each cell 1-seeded, or 1-loculate with 1 seed due to abortion, usually sessile on the slightly accrescent gonophore, lappaceous, the spines elongating from the pericarp at the bases of the spinules; seeds compressed-ovoid or pyriform, with a more or less prominent funicular groove, the cotyledons folded, the endosperm oily.

Standard species: *Triumfetta Lappula* L.

KEY TO THE SERIES

A. Hyaline spinules of ovary straight, in fruit either straight or slightly deflexed, or consisting of 3–5 stellately arranged; ovaries 2-merous; stamens 20–60, most of the species with 40 or more; usually small trees 3–5 m. tall.
  B. Each spine with 3–5 stellately arranged spinules; mature floral buds pandurate ..... STELLATAE (p. 334).
  BB. Each spine with 1 straight or slightly deflexed spinule; mature floral buds oblongoid or obovoid ..... GENICULATAE (p. 336)
AA. Hyaline spinules of ovaries and fruits arcuately recurved; ovaries 3- or rarely 2-merous; stamens 5–40, most of the species with less than 30; usually shrubs 1–3 m. high ..... UNCINATAE (p. 349)

SERIES STELLATAE Sprague & Hutch. in Jour. Linn. Soc. Bot. 39:240. 1909.

1. TRIUMFETTA **stellata** Ko Ko Lay, sp. nov.

Arbores parvae 3 m. altae. Ramuli graciles dense stellato-pubescentes. Folia anguste ovata interdum obscure 3-lobata 5–6 cm. longa 2–3 cm. lata ad basim subtruncata vel subcordata longe acmuinata subdupliciter serrata utrinque pilis sparsis stellatis; petiolis 1–3 cm. longis pilis fulvis stellatis pubescentibus. Inflorescentiae axillares, cymis cymulis 4–5, pedunculis plerumque 4–6 mm. longis, pedicellis 2–3 mm. longis. Flores hermaphroditi, alabastro maturo pandurato 8–9

Fig. 5. *Triumfetta stellata*

mm. longo; sepalis ellipticis circiter 10 mm. longis extra minute stellato-puberulentis, appendiculis circiter 0.25 mm. longis; petalis obovatis brevissimis 2–3 mm. longis, unguilo 1.0–1.5 mm. longo extra breviter villoso; gonophoro circiter 1.5 mm. longo, glandulis ellipticis circiter 1.0 mm. longis 0.5 mm. latis; urceolo 0.3 mm. alto 5-lobato breviter ciliato; staminibus 25–30, filamentis usque ad 5–7 mm. longis glabris; ovario breviter oblongo-ellipsoideo circiter 1 mm. longo, spinulis 35–40 erectis, stylo glabro 2–3 mm. longo, stigmate breviter 2-fido. Fructus globosi non dehiscentes, corpore ipso 3 mm. diametro 2-loculari, loculis 1-spermis cano-tomentosis, aculeis 2–3 mm. longis inaequilater breviter pubescentibus, spinulis 3–5 per aculeo; seminibus maturis haud visis.

MEXICO: MÉXICO: Temascaltépec, Las Mesas, alt. 2000 m., Oct. 25, 1933, *Hinton 4460* (HOLOTYPE in Herb. Kew.).

The affinities of this very distinct species are doubtful. It has a superficial resemblance to *T. Galeottiana*, but can be recognized easily in fruit by the 3 to 5 stellately arranged spinules on the spines, and in flower by its pandurate floral buds with very small obovate petals, which also have small foveae at about the tip of the claw.

SERIES GENICULATAE Sprague & Hutch. in Jour. Linn. Soc. Bot. 39:240. 1909.

KEY TO THE SPECIES

A. Sepals at anthesis 2–4 cm. long; mature fruit body 4–10 mm. in diameter.
  B. Sepals at anthesis 3.5–4.0 cm. long, the apical appendages 1–3 mm. long; spines 4 mm. long or more, densely plumose.
    C. Leaves broadly elliptical to obovate, the petioles about 1 cm. long or less; petals broadly obovate, subequalling the sepals; fruit easily dehiscent, 1.2–3.0 cm. wide including the spines, the spines 0.6–1.0 cm. long; southern Mexico and Honduras..... 2. *T. polyandra*
    CC. Leaves ovate to 3-lobed, the petioles 3–5 cm. long; petals elliptical, less than half the length of the sepals; fruit indehiscent, 1.0–1.5 cm. wide including the spines, the spines 3–5 mm. long; southern Mexico to Panama..... 3. *T. speciosa*
  BB. Sepals at anthesis 2.0–2.5 cm. long, the apical appendages about 1 mm. long; spines 2–3 mm. long, lightly pubescent to glabrescent (not known in *T. cucullata*).
    C. Leaves 11–15 cm. long, the petioles with 2–4 prominent spherical glands at the basal sinus; petals broadly obovate, about 22 mm. long.
      D. Leaves elliptical, acute, the petioles about 1.5 cm. long; stamens 20; coastal west-central Mexico..... 4. *T. cucullata*
      DD. Leaves broadly ovate to 3-lobed, acuminate, the petioles 4–6 cm. long; stamens 40; southwestern Mexico..... 5. *T. coriacea*
    CC. Leaves 5–7 cm. long, the petioles without glands at the basal sinus; petals elliptical to narrowly obovate, 1.2–1.6 cm. long; western Mexico..... 6. *T. Goldmani*
AA. Sepals at anthesis 0.4–1.6 cm. long; mature fruit body 2–3.5 mm. in diameter.
  B. Sepals at anthesis 1.0–1.6 cm. long; fruit body oblongoid, the spines 25 or fewer.
    C. Stem and petioles densely ferruginous-tomentose; leaves pubescent on both surfaces, densely so beneath; sepals densely tomentose without; mature fruit tomentose, 2-loculate, the spines 3–5 mm. long; Colombia..... 7. *T. caudata*
    CC. Stem and petioles glabrescent; leaves essentially glabrous on both surfaces; sepals nearly glabrate without; mature fruit glabrate, 1-loculate, the spines 1–2 mm. long; central Mexico.... 8. *T. Hintonii*
  BB. Sepals at anthesis 0.4–1.0 cm. long; fruit body globose or subglobose, the spines 50 or more.
    C. Petals 1–2 mm. long; leaves densely tomentose; spines plumose, the fruit densely tomentose (not known in *T. ferruginea*).
      D. Apical appendages of the sepals nearly obsolete; leaves cuneate to rounded at the base, rarely subcordate; Honduras and El Salvador..... 9. *T. Calderoni*
      DD. Apical appendages of the sepals manifest; leaves distinctly cordate.
        E. Inflorescences hermaphrodite; sepals 7–10 mm. long; style 4–6 mm. long.
          F. Flowering peduncles 2–4 mm. long; floral buds obovoid; stamens 40–60.
            G. Apical appendages of the sepals 2–3 mm. long, plumose; stamens about 60; stigma undivided; southern Mexico.. 10. *T. ferruginea*

GG. Apical appendages of the sepals about 1 mm. long, lightly pubescent; stamens 40–50; stigma 2-lobed; Costa Rica and Panama ..... 11. *T. arborescens*
FF. Flowering peduncles about 1 mm. long; floral buds oblongoid; stamens about 20; Colombia ..... 12. *T. persimilis*
EE. Inflorescences gynodioecious; pistillate sepals 4–5 mm. long; style about 2 mm. long; southern Mexico ..... 13. *T. dioica*
CC. Petals 3–7 mm. long; leaves glabrescent; spines and fruits glabrate (not known in *T. attenuata*).
D. Leaves long-attenuate, the veins on lower surfaces glabrate; sepals essentially glabrous without, the apical appendages about 2 mm. long; stamens 60; style about 6 mm. long; southern Mexico ..... 14. *T. attenuata*
DD. Leaves shortly acute to acuminate, the veins on the lower surfaces pubescent; sepals lightly stellate-pubescent without, the apical appendages less than 1 mm. long to nearly obsolete; stamens 40; style about 2 mm. long; southwestern Mexico .... 15. *T. Mexiae*

2. TRIUMFETTA POLYANDRA DC. Prod. 1:508. 1824. (T.: based on Sessé & Mociño's *tab. 117* in Herb. Genève).[34]

Triumfetta obovata Schlecht. et Cham. in Linnaea 5:288. 1830. (T.: *Schiede & Deppe s. n.*).
Triumfetta insignis S. Wats. in Proc. Am. Acad. 22:400. 1887. (T.: *E. Palmer 152*).

Small trees or large shrubs about 3–4 m. high; branches and inflorescence axes very densely tomentose with long ferruginous hairs. Leaves broadly elliptical to obovate, 13–15 cm. long and 10–12 cm. wide, the base rounded or subcordate, the tip abruptly acuminate, doubly and regularly serrate, both surfaces scabrous, rather densely tomentose with both simple and stellate hairs; petioles short, stout, about 1 cm. long, covered rather densely with long hairs. Inflorescences on axillary and terminal branches, the cymes of 2–3 cymules, the flowering peduncles 5–9 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds oblongoid, 30–35 mm. long slightly before anthesis, the apical appendages 1–3 mm. long; sepals narrowly obovate, about 36 mm. long, covered rather densely with many long coarse hairs without; petals broadly obovate, showy, 2.7–3.2 cm. long and 5–6 mm. wide, the claw 5–6 mm. long, densely plumose; gonophore short and stout, about 0.75 mm. long and 2.0 mm. thick, the glands oblong, subequalling the gonophore; urceolus about 0.75 mm. high, many-lobed, lightly ciliate; stamens 40–50, the filaments glabrous; ovary spheroid, 3 mm. long, the style 25–28 mm. long, the stigma acute. Fruit spherical, easily dehiscent, the body 6–10 mm. in diameter, densely plumose, 4-loculate, each 2-seeded, the spines numerous, 6–10 mm. long, densely plumose with long hyaline or ferruginous hairs, the spinules erect; seeds ovoid, about 2 mm. long and wide.

Rather rare plants which grow in open forests, usually upon rocky mountain slopes at altitudes of 800–1500 m. in southern Mexico and northern Honduras; flowering from August to September, the fruit maturing from late October and persisting on the plant until early December.

[34] Hochr. in Ann. Conserv. Jard. Bot. Genève 18:110. 1914.

MEXICO: CHIAPAS: Chacomuselo, alt. 800 m., *Matuda 4436*(Mo). JALISCO: Río Blanco, *E. Palmer 152* (Mo, US), *252* (US); slopes of barranca near Guadalajara, *Pringle 4469* (BR, Mo); bluffs near Guadalajara, alt. 5000 ft., *Pringle 9694* (Mo, US); on the road between Colotlán and Bolaños, *Rose 2822* (NY). MÉXICO: Temascaltépec, Luvianos, alt. 1300 m., *Hinton 5900* (US). NAYARIT: Tépic, between Pedro Paula and Acuponeta, *Rose 1927* (NY). VERA CRUZ: Mirador and vicinity, *Liebmann 512, 521* (US), alt. 3500 ped., *Linden Suppl. 26* (BR), *47* (BR, G); Cordillera, Zacuapán, alt. 2000–3000 ped., *Galeotti 7062* (BR).

HONDURAS: YORO: Aguan River valley, vicinity of Coyoles, alt. 1000 ft., *Yuncker, Koepper & Wagner 8167* (Mo).

This species is very distinct and can be easily recognized by its large showy flowers, the largest known for the genus, and also by the extremely characteristic large, easily dehiscent fruits with many long very plumose spines. De Candolle based his description on the sketch of Sessé and Mociño. I have seen a photograph of the original sketch and have no difficulty in recognizing that *T. insignis* of S. Watson is conspecific with it. I have not seen the type of *T. obovata*, but my interpretation of that species is based on the original description, which was later amplified by Turczaninow on Linden's Supplementary Collection No. 47, which I have seen.

3. TRIUMFETTA SPECIOSA Seem. Bot. Voy. Herald, 86. 1853. (T.: *Seemann 1240*).

Triumfetta macrocalyx Turcz. in Bull. Soc. Nat. Moscou 31[1]:230. 1858. (T.: *Linden Suppl. 25*).

Triumfetta micropetala Hochr. in Ann. Conserv. Jard. Bot. Genève 18:98. 1914. (T.: *Linden Suppl. 25*).

Small trees or large shrubs 3–4 m. high; branches and inflorescence axes scurfy, densely covered with ferruginous tomentum. Leaves broadly ovate, generally 3-lobed, 6–9 cm. long and 5–7 cm. wide, the base rounded or subcordate, the middle lobe long-attenuate, the laterals short and blunt, the serrations very irregular, usually blunt and often glandular, the upper surface dark green, coarse with many short stellate hairs, the lower pallid, densely tomentose; petioles 3–5 cm. long, lightly pubescent. Inflorescences axillary, the cymes of 1–2 cymules, usually opposite the bracts, the flowering peduncles 4–5 mm. long, the pedicels 6–8 mm. long. Flowers hermaphrodite, large, the buds oblongoid, 30–35 mm. long slightly before anthesis, the apical appendages about 2 mm. long; sepals narrowly elliptical, about 35 mm. long with many separate tufts of long stellate hairs without; petals ovate, short, about 6 mm. long, the claw about 3–4 mm. long, very densely plumose; gonophore about 1 mm. long and 2 mm. wide, the glands spherical, subequalling the gonophore; urceolus short, about 0.5 mm. high, many-lobed, lightly ciliate; stamens 20, the filaments glabrous; ovary ovoid, about 1.5 mm. long, the style 30–34 mm. long, with many short separate tufts of stellate hairs, the stigma acute. Fruit orbicular, the body 6–8 mm. in diameter, rather densely pubescent, 4-loculate, each cell 2-seeded, on maturity with 8 distinct 1-seeded locules, the spines numerous, 100 or more, each 3–4 mm. long, densely plumose with short hairs, the spinules erect; seeds ovoid, about 2.0 mm. long and wide.

A species of relatively scattered distribution, which extends from southern Mexico to Panama; usually growing in open areas on slopes of mountains, or along the rocky banks of streams at altitudes of 1300–1700 m.; flowering from late July to September, the fruit persisting on the plants until late February or March.

MEXICO: CHIAPAS: Siltepec, *Matuda 1581* (Mo). JALISCO: San Sebastián, trail to El Ranchito, alt. 1500 m., *Mexia 1444* (Mo, US). VERA CRUZ: Mirador, *Linden Suppl. 25* (BR, FM photo); Zacuapán and vicinity, *Purpus 1918* (Mo, NY, US), *3749* (Mo, UC); Cordillera, locality not mentioned, *Galeotti 1973* (BR), *4162* (BR).

BRITISH HONDURAS: Vaca Falls District, *Record s. n.* (US).

GUATEMALA: ALTA VERAPAZ: Patal, alt. 1600 m., *Tuerckheim II 1546* (Mo); San Cristóbal, *Tejada 265* (US).

HONDURAS: MORAZAN: La Montañita, alt. 1400 m., *Williams & Molina R. 10636* (Mo); Mt. Uyuca, alt. 1600 m., *Williams & Molina R. 10252* (Mo).

PANAMA: CHIRIQUÍ: Boquete, *Seemann 1240* (K); Volcán de Chiriquí, Boquete Distr., alt. 7000 ft., *Davidson 515, 895* (Mo); Finca Lérida to Boquete, alt. 1300–1700 m., *Woodson, Allen & Seibert 1115* (Mo).

This species is characterized by its very large flowers and disproportionally short petals, and also by its large fruits with briefly plumose spines. It is rather interesting to note that both the species of Turczaninow and Hochreutiner are primarily based on *Linden Suppl. 25*, a sheet which was apparently examined also by Seemann, as he cites a Linden collection from Vera Cruz, Mexico.

4. TRIUMFETTA CUCULLATA Fernald, in Bot. Gaz. 20:532. 1895. (T.: *Lamb 579*).

Shrubs about 2–3 m. high; lower branches sparingly pubescent, the upper and the inflorescence axes densely cinereous-tomentose. Leaves elliptical, about 13–15 cm. long and 4–5 cm. wide, the base obtuse, with 4 spherical glands at the basal sinus, the serrations generally glandular, the upper surface lightly stellate-pubescent, the lower more densely so; petioles 1.0–1.5 cm. long, densely tomentose. Inflorescences axillary, the cymes of 3 cymules, generally condensed, the flowering peduncles about 3 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 22–24 mm. long slightly before anthesis, constricted slightly above the base, the apical appendages slender, 0.5–1.0 mm. long, very lightly pubescent; sepals oblong, 22–25 mm. long including the apical appendages, stellate-tomentose without, glabrescent within; petals broadly obovate, about 23 mm. long and 6–7 mm. wide, the claw about 4–5 mm. long, densely plumose; gonophore short and stout, about 1.5 mm. long and 2–3 mm. wide, the glands quadrangular, broad, about 1.0 mm. long and 1.5 mm. wide; urceolus short, about 0.5 mm. high, distinctly many-lobed, briefly ciliate; stamens 20, the filaments smooth, densely pubescent at the base; ovary orbicular, about 1.5 mm. long, the spinules about 50, erect, the style about 22 mm. long, the stigma acute. Fruit not seen.

Known only from the type. Flowers in February.

MEXICO: NAYARIT: Tépic, Zopelote, alt. 2000–3000 ft., *Lamb 579* (Mo, US).

Though very imperfectly known, this species may be easily identified by its short-petiolate elliptic leaves, by its large showy flowers, and also by its possession of only 20 stamens with the filaments densely pubescent at the base.

5. TRIUMFETTA CORIACEA Hochr. in Ann. Conserv. Jard. Bot. Genève 18:108. 1914. (T.: *Langlassé 815*).

Small trees or large shrubs 3–4 m. high; branches and inflorescence axes glabrescent, brownish. Leaves broadly ovate to 3-lobed, 11–14 cm. long and 8–12 cm. wide, the base cuneate to rounded, the tip long-acuminate; the serrations regular and usually double, the upper surface glabrate, the lower very lightly pubescent to glabrescent; petioles stout, 4–6 cm. long, with 2 or 4 prominent glands at the basal sinus. Inflorescences axillary, rarely terminal, the cymes of 2–3 cymules, borne very loosely in nodose clusters, the flowering peduncles 6–8 mm. long, the pedicels 2–4 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, about 22 mm. long slightly before anthesis, constricted in the middle, the apical appendages very short, about 0.5 mm. long; sepals elliptical, 22–24 mm. long, rather lightly stellate-pubescent without; petals broadly obovate, 20–22 mm. long and 6–8 mm. wide, the claw about 3 mm. long, densely plumose; gonophore slender, 1–2 mm. long, the glands elliptical, subequalling the gonophore; urceolus about 0.5 mm. high, many-lobed, lightly ciliate; stamens about 40, the filaments glabrous; ovary ovoid, about 1.5 mm. long, the spinules numerous, erect, the style about 22 mm. long, the stigma acute. Immature fruit orbicular, the body essentially glabrous, 2-loculate, each cell 1-seeded, the spines numerous, rather short; mature fruit not seen.

Southwestern Mexico, usually growing on hillsides in pine and oak forests at altitudes of 800–1000 m.; flowering from middle of December to late January.

MEXICO: GUERRERO: San Vincente de San Juan, alt. 920 m., *Hinton 11193* (GH); Plan de Carrizo, Galeana, alt. 850 m., *Hinton 11056* (GH); Sierra Madre, alt. 800 m., *Langlassé 815* (G, GH, US).

This species can be recognized by its glabrescent, broadly ovate to 3-lobed leaves with 2–4 spherical glands on the petioles at the basal sinus; and also by its large, showy flowers with deep yellow broadly obovate petals. It is unfortunate that mature fruiting specimens are unavailable.

6. TRIUMFETTA GOLDMANI Rose, in Contr. U. S. Nat. Herb. 12:285. 1909. (T.: *Goldman 264*).

Triumfetta sanctae-luciae Sprague, in Kew Bull. 114. 1923. (T.: *Seemann 2147*).
Triumfetta quercetorum Bullock, loc. cit. 295. 1937. (T.: *Hinton 6746*).

Small trees or large shrubs 3.0–3.5 m. high; branches and inflorescence axes with many short stellate hairs, later becoming glabrate. Leaves elliptical to narrowly ovate, 5–7 cm. long and 2–3 cm. wide, the base cuneate or rounded, the tip narrowly and gradually long-attenuate, the serrations rather regular, both surfaces scabrous with many short stellate and simple hairs; petioles slender, 1.0–1.5 cm. long, rather lightly but coarsely pubescent; bracts of the same general shape as the vegetative leaves. Inflorescences axillary, rarely terminal, the cymes of 1–2 cymules, always in the axils of the bracts, the flowering peduncles 4–6 mm. long, the pedicels about 4 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 18–20 mm. long and 2–3 mm. wide slightly before anthesis, the apical

appendages slender, 1–2 mm. long; sepals narrowly ovate, about 20 mm. long, with few separate tufts of short stellate hairs without; petals elliptical to narrowly obovate, 12–16 mm. long and about 3 mm. wide, the claw 4–5 mm. long, densely plumose; gonophore large, about 2.5 mm. long and 1.5 mm. wide, the glands elliptical, subequalling the gonophore; urceolus short, about 0.25 mm. high, many-lobed, lightly ciliate; stamens 20, the filaments glabrous, ovary orbicular, about 1.5 mm. long, the spinules about 75, erect, the style about 16 mm. long, the stigma either acute or briefly bifid. Fruit spheroid, the body 4–5 mm. in diameter at maturity, lightly pubescent, 4-loculate, each cell 1-seeded, the spines falcate, about 75, 2–3 mm. long, lightly pubescent with few short hairs; seeds pyriform, about 1.5 mm. long and wide.

Rather common plant of western and central Mexico, usually growing in oak and pine forests in shady slopes under trees in moist places or on edges of meadows along streams at altitudes of 600 to 2000 m.; flowering in September and October, the fruit persisting until late January.

MEXICO: CHIHUAHUA: Arroyo Hondo, Sierra Charuco, *Gentry 1768* (Mo, US); San José de Pinál, Río Mayo, *Gentry 2841* (Mo); Guicorichi, Río Mayo, alt. 5000 ft., *Gentry 1967* (Mo); El Carrizo, alt. 800 m., *Ortega 6011* (US); Balboa, *Ortega 5043* (US). DURANGO: Sierra Tres Picos, alt. 3500 ft., *Gentry 5296* (Mo); La Bajada, Tamazula, alt. 300 m., *Ortega 4252* (US). GUERRERO: Mina, Zihuagio-Ojo de Agua, alt. 1640 m., *Hinton 9710* (US); Mina, Chiriagua, alt. 1600 m., *Hinton 9847* (GH), *10663* (GH, Mo, US); Pilas Filo Mayor, alt. 1800 m., *Hinton 10750* (GH, US); Chilacayote-Espadinas, alt. 1500 m., *Hinton 14927* (GH, US). MÉXICO: Temascaltepec: Rincón del Carmen, alt. 1340 m., *Hinton 1953* (Mo); Nanchititla, *Hinton 3082* (GH, K), *4962* (K); Pungarancho, alt. 950 m., *Hinton 5253* (Mo, US), *6746* (GH, K, Mo, US); Ypericones, *Hinton 6996* (Mo, US). MICHOACAN: Coalcomán: Salitre-mesa, alt. 1780 m., *Hinton 12492* (GH, US); Pto. Zarzamora, alt. 1660 m., *Hinton 12262* (GH, US). SINALOA: Santa Lucia, alt. 1200 m., *Seemann 2147* (GH, K); Sierra de Choix, 50 miles n. e. of Choix, *Goldman 264* (US); Cerro de la Sandia, northeast of Panuco, alt. 1800–2000 m., *Pennell 20121* (US); Quebrada de Mansana, Sierra Suratato, alt. 4000–4500 ft., *Gentry 6582* (Mo); Sierra Madre Mts., "El Batél", alt. 4000 ft., *Mexia 431* (Mo); Quebrada Chica, San Ignacio, alt. 1380 m., *Narvaez & Salazar 100* (US). SONORA: Arroyo del Agua Blanco, Dist. Álamos, *Gentry 506M* (US).

The fruits of this species are very characteristic, being spheroid with about 75 falcate, lightly pubescent spines. Though the spines are slightly recurved the spinules are erect. The small elliptical to narrowly ovate leaves and the relatively large flowers with yellow, narrowly obovate petals make this species convenient to identify. The leaves of the type of *T. quercetorum* are very slightly more pubescent than those of *T. Goldmani*, but in both they are nearly glabrate and the variation is only slight.

7. TRIUMFETTA CAUDATA Tr. & Planch. in Ann. Sci. Nat. Bot. IV, 17:353. 1862. (T.: "Río Hacha", *Purdie s. n.* in Herb. Kew.).

Small trees or shrubs 2–3 m. high; branches and inflorescence axes covered very densely with rich orange-brown simple and stellate hairs. Leaves broadly ovate, 11–15 cm. long and 8–10 cm. wide, the base rounded to subcordate, the tip gradually and narrowly long-attenuate, the serrations blunt, small, usually double and regular, the upper surface scabrous, lightly pubescent, the veins more

densely so, the lower rather densely tomentose with both stellate and simple hairs; petioles 3–5 cm. long, densely covered with orange-brown hairs. Inflorescences axillary, the cymes of 2–3 cymules, usually in the axils of the bracts, the flowering peduncles 4–5 mm. long, the pedicels 3–4 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 10–15 mm. long slightly before anthesis, the apical appendages 1–2 mm. long, densely pubescent; sepals oblong, 12–16 mm. long with dense orange-brown pubescence without; petals narrowly obovate, subequalling the sepals, the claw 2–3 mm. long, rather densely plumose; gonophore short, about 0.5 mm. long, the glands small, spherical; urceolus about 0.5 mm. high, many-lobed, densely ciliate; stamens 20–25, the filaments glabrous; ovary ovoid, about 0.75 mm. high, the spines 40–50, erect, the style 7–8 mm. long, the stigma acute. Fruits oblongoid, the body 2–3 mm. in diameter and 3–5 mm. long at maturity, densely pubescent with many short stellate and simple hairs, 2-loculate, each cell 1-seeded, the spines 20–25, each 3–5 mm. long, densely plumose with short grayish hairs; seeds ovoid, about 1.5 mm. long and wide.

Apparently rare plants known only from Colombia, where they grow on the borders of forests and open grasslands at altitudes of about 750 m.; flowering from October to December, and the fruits maturing in January and February.

COLOMBIA: MAGDALENA: près de Molina, Río Hacha, *Purdie s. n.* (K); Minca, *Apolinar 627* (US). SANTA MARTA: Onaca, alt. 2500 ft., *H. H. Smith 1688* (G, Mo, NY, UC, US), *1907* (Mo, NY).

This is an extremely distinct species, and is characterized by its branches and petioles being densely covered with lustrous ferruginous tomentum, by the leaves which are profoundly cordate with long attenuate tips, by the large and spreading inflorescences, and also by its small ellipsoid fruits with about 25, rather densely tomentose spines.

8. TRIUMFETTA HINTONII Sprague, in Kew Bull. 294. 1937. (T.: *Hinton 7018*).

Small trees 2.5–6.0 m. high; branches and inflorescence axes very lightly pubescent, glabrescent. Leaves broadly ovate to elliptical, 8–11 cm. long and 3–5 cm. wide, the base cuneate to rounded on younger ones, subcordate on more mature ones, the tip gradually and narrowly acuminate, the serrations small, blunt, usually double and regular, the upper surface dark green, very lightly pubescent to nearly glabrate, the lower pallid, slightly more pubescent than the upper; petioles 2–3 cm. long, lightly pubescent. Inflorescences axillary, the cymes of 2 cymules, usually opposite the bracts, the flowering peduncles 3–5 mm. long, the pedicels 2–3 mm. long. Flowers hermaphrodite, the buds oblongoid, 9–11 mm. long at anthesis, the apical appendages very small, nearly obsolete; sepals oblong, 10–12 mm. long, lightly stellate-pubescent without; petals narrowly obovate, 6–7 mm. long, the claw very distinct with a constriction at the tip, about 3 mm. long, densely plumose; gonophore slender, about 2 mm. long, the glands oblong, about half the length of the gonophore; urceolus short, about 0.5 mm. high, 5-lobed, lightly ciliate; stamens 15–20, the filaments smooth, glabrous; ovary ellipsoid, about 1.5 mm. long, the spinules 40–50, erect, the style about 6 mm. long, the

stigma acute, sometimes briefly 2-lobed. Fruit ellipsoid, the body about 6 mm. long and 3.0–3.5 mm. wide at maturity, glabrous, 2-loculate, each cell 1-seeded, but only one maturing, the other aborting completely, the spines slightly falcate, short, 1–2 mm. long, only 10–16 remaining at maturity; seeds pyriform, about 2.5 mm. long and 1.5 mm. wide.

Known only from central Mexico, growing in pine and oak forests, along streams at altitudes of 2000–2400 m.; flowering from June to September, the fruit maturing from October to November.

MEXICO: MÉXICO: Temascaltépec: La Labór, alt. 2000 m., *Hinton 3837* (K, US); Cajones, alt. 2480 m., *Hinton 4224* (K); Nanchititla, *Hinton 5324* (K, US); La Labór, *Hinton 6594* (GH, Mo, US); Cumbre de Tejupilco, *Hinton 7018* (K, Mo, US); Pantoja, *Hinton 7027* (Mo, US). MICHOACAN: Coalcomán, Sierra Torricillas, alt. 2140 m., *Hinton 12343* (GH).

This species has very characteristic fruits. The flower is quite normal for the genus, bearing a 2-loculate ovary with 40–50 straight-pointed spinules. After fertilization, most of the spines fail to develop at the bases of the spinules; thus the mature fruit body becomes rugose in places where the spines have not elongated sufficiently; furthermore, one of the locules aborts completely, and only one 1-seeded locule matures. In their oblongoid fruits and also in their marked tendency towards having a smaller number of spines on the fruit than of spinules on the ovaries, *T. Hintonii* and *T. caudata* are closely related.

9. TRIUMFETTA CALDERONI Standl. in Jour. Wash. Acad. 14:98. 1924. (T.: *Calderón 78*).

Small trees or large shrubs 6–8 m. high; branches and inflorescence axes covered densely with both fine stellate and long spreading coarse stiff hairs. Leaves broadly ovate to obscurely 3-lobed, 10–15 cm. long and 7–11 cm. wide, the base rounded or subcordate, the tip gradually and narrowly long-acuminate, the serrations coarse and irregular, blunt and usually glandular, the upper surface dark green, lightly but coarsely pubescent with many short suppressed stellate hairs, the lower pallid, densely pubescent with long spreading stellate and simple hairs; petioles 5–7 cm. long, densely pubescent; bracts elliptical. Inflorescences terminal, large and spreading, with many small, caducous bracts, the cymes of 4–6 cymules, rather lax in flower though generally crowded in fruit, the flowering peduncles about 3–4 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly obovoid, constricted towards the base, about 5 mm. long at anthesis, the apical appendages very small to nearly obsolete; sepals elliptical, 5–7 mm. long, whitish and densely tomentose without, yellow-brown and glabrescent within; petals obovate, small, about 2 mm. long, the claw very short, lightly plumose; gonophore short and stout, about 0.5 mm. long and 1.5 mm. wide, the glands very small, spherical; urceolus about 0.25 mm. high, many-lobed, lightly ciliate; stamens 40, the filaments glabrous; ovary ovoid, about 1 mm. long, the spinules about 50, erect, the style 2–3 mm. long, the stigma acute. Fruit spheroid, the body 2–3 mm. in diameter at maturity, rather densely tomentose, 2-loculate, each cell 1-

seeded, the spines about 50, 4–5 mm. long, densely plumose with relatively long stiff white hairs; seeds pyriform, about 1.0 mm. long and wide.

Common weedy plant of Honduras and El Salvador, chiefly found in dry rocky thickets at altitudes of 450–1000 m.; flowering in October, the fruit maturing in late December to January.

HONDURAS: CHOLUTECA: San Marcos, alt. 1000 m., pine forest area, *Williams & Molina R. 10923* (Mo). EL PARAÍSO: 8 kms. west of Ojo de Agua, *Williams & Molina R. 10676* (Mo). MORAZÁN: San Antonio, road near Zamorano, *Williams & Molina R. 11160* (Mo).

EL SALVADOR: SAN JOSÉ: *Calderón 1929* (GH, US). SAN SALVADÓR: vic. Tonacatepeque, *Standley 19475* (GH, US); vicinity of San Salvadór, alt. 650–850 m., *Standley 22782* (GH, US); San Salvadór, *Calderón 78* (GH, US), *354* (US), *1257* (GH, Mo, US). DATA INCOMPLETE: *Choussy 55* (US).

This species can be recognized in fruit by its long slender, rather densely plumose spines, and in flower by the absence of apical appendages on the sepals, and also by the short petals.

10. TRIUMFETTA **ferruginea** Ko Ko Lay, sp. nov.

Ramuli graciles dense pubescentes pilis ferrugineis et stellatis et simpilicibus. Folia late ovata interdum 3-lobata 6–7 cm. longa 5–7 cm. lata base profunde cordata apice longe acuminata supra pilis sparsis stellatis, infra dense canescentia vel ferrugineo-tomentosa; petiolis 3–4 cm. longis dense ferrugineo-tomentosis. Inflorescentiae terminales, cymis circiter 6 cymulis in axillis bractearum dense confertis, bracteis ellipticis vel lanceolatis, pedunculis plerumque 3 mm. longis, pedicellis 1–2 mm. longis. Flores hermaphroditi, alabastro maturo obovoideo 6–7 mm. longo; sepalis ellipticis 7–9 mm. longis extra breviter denseque stellato-pubescentibus, appendiculis circiter 2 mm. longis dense plumosis; petalis obovatis brevissimis 1.5–2.0 mm. longis, unguilo circiter 0.5 mm. longo extra dense plumosa; gonophoro circiter 0.5 mm. longo 1.5 mm. lato, glandulis quadrangularibus circiter 1.0 mm. longis; urceolo 0.5 mm. alto multilobato breviter ciliato; staminibus 60, filamentis usque 3–4 mm. longis glabris; ovario ovoideo circiter 1 mm. longo, spinulis 30–40 erectis, stylo glabro circiter 4 mm. longo, stigmate acuto. Fructus maturi desunt.

MEXICO: CHIAPAS: Las Pilas, June 2, 1904, *Goldman 1050* (holotype in U. S. Nat. Herb.).

Related to *T. arborescens* from which it may be easily distinguished by its more numerous stamens and much longer apical appendages of the sepals. I have not seen any fruiting specimen of this species.

11. TRIUMFETTA ARBORESCENS (Seem.) Sprague, in Kew Bull. 351. 1923.

Heliocarpus arborescens Seem. Bot. Voy. Herald, 86. 1853. (T.: "Panama," *Seemann s. n.* in Herb. Kew.).

Small trees 5–6 m. high; branches and inflorescence axes scurfy, densely tomentose with short ferruginous stellate hairs. Leaves broadly ovate, usually 3-lobed, 10–13 cm. long and 7–10 cm. wide, the base cordate, the middle lobe long-

Fig. 6. *Triumfetta ferruginea*

attenuate, the laterals acute, the serrations very irregular, the basal ones glandular, the upper surface scabrous, covered lightly with many short stellate hairs, the lower densely tomentose with both simple and stellate hairs, becoming less so at maturity; petioles slender, 6–9 cm. long, densely ferruginous-tomentose. Inflorescences terminal, the cymes of 3–5 cymules, condensed in nodose clusters, the flowering peduncles 2–4 mm. long, the pedicels about 2 mm. long. Flowers hermaphrodite, the buds obovoid, 6–7 mm. long slightly before anthesis, constricted towards the base, the apical appendages about 1 mm. long; sepals broadly

elliptical, 7–10 mm. long, pallid and densely tomentose without, yellow-brown and glabrescent within; petals obovate, short, about 2–3 mm. long, the claw very short, briefly plumose; gonophore slender, about 0.75 mm. long, the glands elliptical, subequalling the gonophore; urceolus about 0.5 mm. high, indistinctly lobed, briefly ciliate; stamens about 50, the filaments smooth, glabrous; ovary ovoid, about 0.75 mm. long, the spinules about 75, erect, the style about 5 mm. long, the stigma very briefly 2-fid. Fruit suborbicular, the body 2–3 mm. in diameter and 3–4 mm. long at maturity, cinereous-pubescent, 2-loculate, each cell 1-seeded, the spines about 75, 3–4 mm. long, reddish-brown, shortly plumose; seeds pyriform, about 0.75 mm. long and wide.

COSTA RICA: GUANACASTE: vicinity of Tilarán, alt. 500–650 m., *Standley & Valerio 45709* (US).

PANAMA: COCLÉ: between Paso del Arado and Olá, in savannahs and thickets, alt. 20–280 m., *Pittier 5017* (US). DATA INCOMPLETE: *Seemann 96* (GH), *s. n.* (K); *Cowell 239* (NY).

Rather rare small trees of Costa Rica and Panama; flowering in December and the fruit maturing in January and February.

12. TRIUMFETTA **persimilis** Ko Ko Lay, sp. nov.

Frutex circiter 1 m. altus. Ramuli graciles dense pubescentes, pilis ferrugineis et stellatis et simplicibus. Folia late ovata vel 3-lobata 10–14 cm. longa 8–10 cm. lata base profunde cordata apice longe acuminata margine irregulariter serrata interdum glandulosa supra pilis sparse stellatis scabratis, infra dense canescenti-tomentosa; petiolis 3–4 cm. longis dense tomentosis. Inflorescentiae terminales, cymis 3–4 cymulis, bracteis ovatis vel obscure 3-lobatis, pedunculis circiter 1 mm. longis, pedicellis 6–8 mm. longis. Flores hermaphroditi, alabastro maturo oblongoideo 6–8 mm. longo; sepalis ellipticis 7–9 mm. longis extra longe et dense stellato-tomentosis, appendiculis circiter 2 mm. longis dense plumosis; petalis ellipticis, 6–7 mm. longis, unguilo 0.5–1.0 mm. longo extra breviter plumoso; gonophoro circiter 0.25 mm. longo, glandulis quadrangularibus; urceolo 0.25 mm. alto, 5-lobato breviter ciliato; staminibus 20, filamentis usque ad 5–6 mm. longis glabris; ovario ovoideo circiter 1.5 mm. longo, spinulis 70–80 erectis, stylo glabro 3–4 mm. longo, stigmate breviter 2-fido. Fructus globosus non dehiscens, corpore ipso 2–3 mm. diametro, dense canescenti-tomentosus 2-locularis, loculis 2-spermis, aculeis circiter 75, 3–4 mm. longis dense plumosis; seminibus ovoideo-acutis, circiter 1.5 mm. longis et latis.

COLOMBIA: SANTANDER: en terrenos secos y arenosos a orillas del Río Chicamocha, en pescadero, alt. 500 m., Dec. 1948, *Araque & Barkley 18S.286* (holotype in Herb. Mo. Bot. Gard., isotype in U. S. Nat. Herb.).

In flower this species has a superficial resemblance to *T. caudata*, but its fruits are much more strikingly similar to those of *T. Calderoni*. It may be easily recognized by its densely tomentose leaves, small oblongoid floral-bud with only 20 stamens, and by its spheroid fruit with many densely plumose spines.

13. TRIUMFETTA DIOICA T. S. Brandg. in Univ. Calif. Publ. Bot. 10:412. 1924. (T.: *Purpus 9256*).

Small trees about 3 m. high; branches and inflorescence axes covered densely with many long grayish-brown hairs. Leaves broadly ovate to obscurely 3-lobed, 8–11 cm. long and 5–7 cm. wide, the base deeply cordate, the tip gradually and narrowly long-acuminate, the serrations very irregular, usually blunt, the basal ones glandular, the upper surface dark green, scabrous with many long appressed simple and stellate hairs; petioles 4–6 cm. long, slender, densely clothed with long spreading hairs. Inflorescences gynodioecious, the pistillate terminal, the cymes of 4–6 cymules in dense nodose clusters, the flowering peduncles and pedicels about 2 mm. long. Hermaphrodite flower not seen, the pistillate small, the floral bud 3–4 mm. long slightly before anthesis, the apical appendages short, 1 mm. long or less; sepals narrowly elliptical, 4–5 mm. long, pallid and densely tomentose without, yellow-brown and glabrescent within; petals elliptical to narrowly obovate, small, about 1.5 mm. long, the claw nearly obsolete; gonophore short, about 0.5 mm. long, the glands oblong, subequalling the gonophore; urceolus about 0.5 mm. high, many-lobed, briefly ciliate; ovary ovoid, about 1.5 mm. long, the spinules about 50, erect, the style about 2 mm. long, the stigma briefly 2-fid. Fruit spheroid, covered with about 50 slender, densely plumose spines; mature fruit not seen.

Known only from Chiapas, Mexico. Flowers in September.

MEXICO: CHIAPAS: Hacienda Monserrate, *Purpus 9256* (Mo, UC, US); Buena Vista, *Purpus 9285* (UC).

It is unfortunate that this species is so imperfectly known. Due to the lack of mature fruits and hermaphrodite flowers its proper position is rather obscure. It is apparently related to *T. Calderoni* in the possession of small flowers and spheroid fruits with numerous plumose spines.

14. TRIUMFETTA **attenuata** Ko Ko Lay, sp. nov.

Ramuli glabri irregulariter punctati lenticellis multis parvis tecti. Folia late ovata 10–14 cm. longa 6–9 cm. lata base subtruncata vel rotundata apice longe attenuata subdupliciter serrata utrinque glabrata; petiolis gracilibus 6–9 cm. longis glabris. Inflorescentiae terminales, cymis 4–5 cymulis, pedunculis 5–7 mm. longis, pedicellis 4–5 mm. longis. Flores hermaphroditi, alabastro maturo obovato 6–7 mm. longo; sepalis ellipticis vel anguste obovatis 7–9 mm. longis extra glabrescentibus, appendiculis circiter 2 mm. longis glabris; petalis obovatis 6–7 mm. longis, unguilo circiter 1.5 mm. longo dense plumoso; gonophoro circiter 0.75 mm. longo 1.5 mm. lato, glandulis ellipticis 0.5–0.75 mm. longis; urceolo 0.5 mm. alto 5-lobato breviter ciliato; staminibus 60, filamentis usque ad 5–7 mm. longis glabris, spinulis circiter 75 erectis, stylo glabro circiter 6 mm. longo, stigmate acuto. Fructus maturi desunt.

MEXICO: CHIAPAS: Escuintla, Dec. 1936, *Matuda 0488* (holotype in Herb. Mo. Bot. Gard.; isotypes in Herb. Univ. Michigan, and U. S. Nat. Herb.).

This species is most closely related to *T. Mexiae*, from which it may be distinguished easily by its glabrate leaves and floral buds, the much longer apical appendages of the sepals, and its style which is about 6 mm. long with the stigma exserted above the stamens. It is unfortunate that no fruiting material of this species is available.

15. Triumfetta **Mexiae** C. V. Morton & Ko Ko Lay, sp. nov.

Arbores parvae 5–6 m. altae. Ramuli inferne glabrati apicem versus tomentosi pilis multis brevibus stellatis. Folia late ovata 8–11 cm. longa 6–9 cm. lata base cuneata vel rotundata apice longe acuminata subdupliciter serrata utrinque pilis sparsis stellatis mox glabrescentia, nervis subtus pallidioribus pilis brevibus stellatis; petiolis 3–5 cm. longis sparse stellato-pubescentibus. Inflorescentiae terminales, cymis cymulis 4–5, pedunculis 2–3 mm. longis, pedicellis 3–4 mm. longis. Flores hermaphroditi, alabastro maturo obovoideo 5–6 mm. longo; sepalis anguste obovatis 5–8 mm. longis extra breviter stellato-pubescentibus; petalis ellipticis vel anguste obovatis 4–6 mm. longis, unguilo circiter 2 mm. longo dense plumoso; gonophoro circiter 0.75 mm. longo 1.0 mm. lato, glandulis ellipticis circiter 0.75 mm. longis; urceolo 0.25 mm. alto multilobato breviter ciliato; staminibus 40, filamentis usque ad 3–4 mm. longis glabris; ovario ovoideo circiter 1.5 mm. longo, stigmate breviter 2-fido. Fructus globosi non dehiscentes, gynophoro brevi supra gonophorum, corpore ipso 3–4 mm. diametro glabro 2-loculari, loculis 2-spermis, aculeis 75–100 gracilibus glabris; seminibus ovoideo-acutis circiter 2 mm. longis et latis.

A rather common species of southwestern Mexico, growing at altitudes of 1000 to 1200 m.; flowering in September and early October, the fruits maturing from late October to November.

Mexico: guerrero: Sierra Madre del Sur, north of Río Balsas, Distr. Adama, Temisco, barranca below Ore Mill, alt. 1265 m., *Mexia 8834* (holotype in U. S. Nat. Herb.; isotypes in Gray Herb., Herb. Mo. Bot. Gard., and Herb. Univ. Calif.); mountains near Iguala, alt. 2500 ft., *Pringle 9228* (GH, MICH, US); Iguala Cañon, *Pringle 10069½* (GH, MICH, US); between Sochi and Tlalkinsala, alt. 3600–4800 ft., *Nelson 2036* (NY, US); Coyuca-Chacamerito, *Hinton 6621* (US). michoacán: Zitacuaro-La Mora, alt. 1325 m., *Hinton 13230* (GH).

There is a great superficial resemblance in the aspects of the flowering specimens of this species to those of *Heliocarpus occidentalis* Rose. It is, however, quite distinct from other species of *Triumfetta* and can easily be recognized.

Series Uncinatae Sprague & Hutch. in Jour. Linn. Soc. Bot. 39:240. 1909.

KEY TO THE SPECIES

A. Flowers hermaphrodite, the buds oblongoid, the style at least 3 times the length of the ovary; fruits distinctly pubescent.
  B. Petioles usually less than 1.5 cm. long, the leaves elliptical, at least twice as long as broad; southwestern Mexico.
    C. Fruit with more than 100 short, straight, glabrous spines, each about 1 mm. long; sepals at anthesis 13–16 mm. long; stamens 25–30 ..... 16. *T. brevipes*

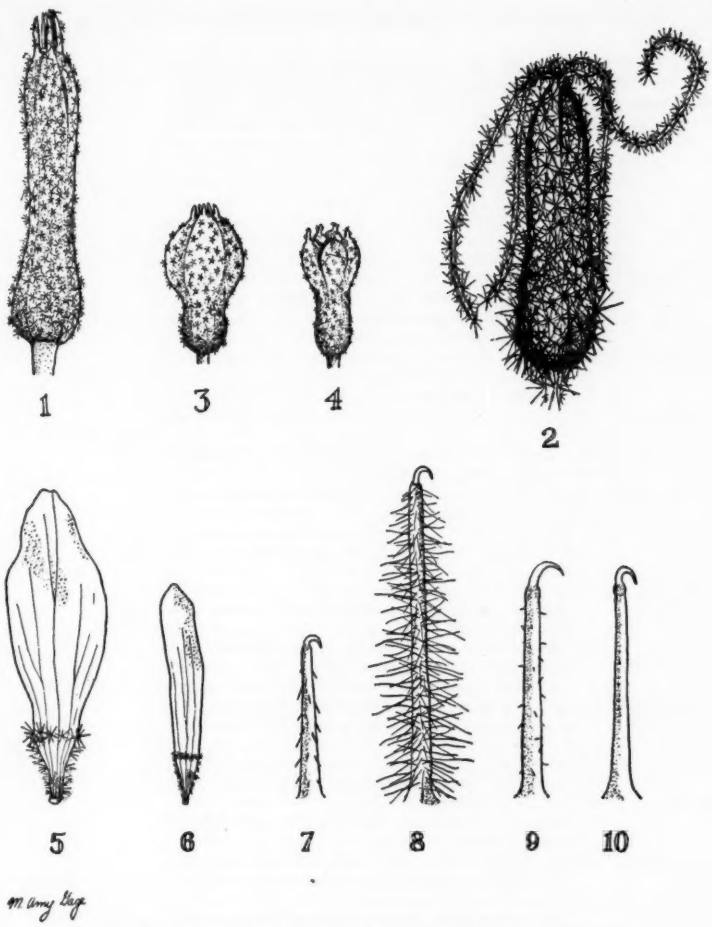

Fig. 7. Illustrations of taxonomic criteria for Series UNCINATAE:

1. Narrowly oblongoid floral bud of *T. Palmeri* with relatively short apical appendages.
2. Narrowly oblongoid floral bud of *T. Purpusii* with very long apical appendages.
3. Obovoid floral bud of *T. Galeottiana.*
4. Younger floral bud of *T. Bartramia* with very deeply cucullate sepals.
5. Broadly obovate petal of *T. bogotensis.*
6. Elliptical to narrowly obovate petal of *T. obscura.*
7. Retrorsely pilosulose spine of *T. semitriloba.*
8. Densely plumose spine of *T. socorrensis.*
9. Irregularly pubescent spine of *T. discolor* with few short hairs.
10. Glabrate spine of *T. paniculata.*

CC. Fruit with less than 75 falcate, pubescent spines, each about 2–3 mm. long; sepals at anthesis 15–20 mm. long; stamens 20.... 17. *T. Palmeri*

BB. Petioles generally much longer than 2.0 cm., the leaves ovate (except in *T. obscura*), usually much less than twice as long as broad.

C. Stamens 20–40 (except *T. Lappula* with 5–15); mature fruit (including spines) 7–15 mm. thick.

D. Spines plumose or irregularly pubescent; sepals at anthesis 1.2–3.0 cm. long.

E. Fruit body oblongoid with about 20 spines, each 6–10 mm. long; sepals at anthesis 12–14 mm. long; Revilla Gigedo Islands, Mexico.... 18. *T. socorrensis*

EE. Fruit body globose with 40 or more spines, each usually 2–5 mm. long; sepals at anthesis 1.5–3.0 cm. long.

F. Fruit with 40–50 spines; apical appendages of the sepals 5–10 mm. long; stamens about 40.

G. Spines densely plumose; apical appendages of the sepals 7–10 mm. long; southeastern Mexico.... 19. *T. Purpusii*

GG. Spines slightly pubescent to nearly glabrate; apical appendages of the sepals 5–7 mm. long; southwestern Mexico.... 20. *T. falcifera*

FF. Fruit with 75–200 spines; apical appendages of the sepals shorter than 3 mm.; stamens 15–30.

G. Leaves densely tomentose on both surfaces; mature fruit 6- to 10-loculate, each cell 1-seeded.

H. Mature fruit 8- or 10-loculate; sepals at anthesis 1.8–2.7 cm. long, the apical appendages 2–3 mm. long.

I. Mature fruit 5- to 10-loculate, the spines and body very shortly pubescent; sepals broadly obovate, the stamens 25–30; Peru.... 21. *T. multilocularis*

II. Mature fruit 8-loculate, the spines and body with long plumose hairs; sepals elliptical to narrowly obovate; stamens 20; Colombia.... 22. *T. mollissima*

HH. Mature fruit 6-loculate; sepals at anthesis about 1.7 cm. long, the apical appendages about 1 mm. long; northeastern Brazil.... 23. *T. longicoma*

GG. Leaves densely tomentose on lower surfaces only or both surfaces lightly pubescent to glabrescent; fruit with 3, 1- to 2-seeded locules.

H. Sepals at anthesis 22–30 mm. long; fruit indehiscent insofar as known.

I. Leaves 11–16 cm. long and 6–9 cm. wide, or slightly larger; fruit stellate-pubescent, spines briefly but distinctly pubescent.

J. Leaves 3-lobed, without tufts of hairs at axils of the veins on the lower surface; filaments lightly stellate-pubescent at the base; spines very lightly pubescent with short hairs; northwestern Mexico.... 24. *T. chihuahuensis*

JJ. Leaves not lobed, with many long tufts of hairs at the axils of the veins on the lower surface; filaments not pubescent; spines rather densely pubescent; west-central Mexico.... 25. *T. barbosa*

II. Leaves 6–8 cm. long and 3–4 cm. wide; fruit tomentose, the spines glabrescent; central and southwestern Mexico.... 26. *T. columnaris*

HH. Sepals at anthesis 15–20 mm. long; fruit easily dehiscent.

I. Leaves distinctly longer than broad, gradually and narrowly acuminate, both surfaces lightly pubescent to glabrescent; fruit with 100 or more slender spines, each about 4 mm. long; southern Mexico and West Indies to northern South America.... 27. *T. grandiflora*

II. Leaves nearly as broad as long, shortly acute to acuminate, tomentose beneath; fruit with about 75 relatively thick spines, each about 2–3 mm. long; northwestern Mexico..... 28. *T. discolor*

DD. Spines retrorsely pilosulose; sepals at anthesis 3–9 mm. long (except *T. bogotensis* and *T. abutiloides* sometimes up to 13 mm. long).

E. Petals present; fruit and flower with a 5-glandular gonophore, the urceolus manifest.

F. Leaves with both stellate and simple hairs, the latter prominent on both surfaces; sepals at anthesis 8–13 mm. long, the petals broadly obovate.

G. Leaves densely tomentose on both surfaces; apical appendages of the sepals nearly obsolete or less than 1 mm. long; fruit with 6, 1-seeded locules at maturity; Haiti and northern South America..... 29. *T. abutiloides*

GG. Leaves lightly pubescent on both surfaces; apical appendages of the sepals 2–3 mm. long; fruit with 3, 2-seeded locules at maturity; pantropical..... 30. *T. bogotensis*

FF. Leaves with stellate pubescence only; sepals at anthesis 5–9 mm. long, the petals linear to narrowly obovate.

G. Leaves and bracts narrowly elliptical, at least twice as long as broad; northeastern South America..... 31. *T. obscura*

GG. Leaves ovate, generally 3-lobed, less than twice as long as broad, the bracts elliptical.

H. Leaves slightly pubescent, glabrescent; petals less than half the length of the sepals; mature fruit body about 3 mm. thick; western Mexico..... 32. *T. acracantha*

HH. Leaves coarsely stellate-pubescent; petals subequalling the sepals; mature fruit body usually 4 mm. thick or more.

I. Petioles with 4 prominent glands on the basal sinus; mature fruit 8- to 10-loculate, the spines numerous, about 200; Trinidad and northern South America..... 33. *T. althaeoides*

II. Petioles without glands at the basal sinus; fruit 3-loculate, the spines 75 or fewer.

J. Apical appendages of the sepals 2 mm. long or less; fruit body lightly to densely pubescent, spines about 75; pantropical..... 34. *T. semitriloba*

JJ. Apical appendages of the sepals 3 mm. long or more; fruit body tomentose, the spines 25–40; Ecuador and Peru..... 35. *T. oligacantha*

EE. Petals absent; gonophore and urceolus obsolete in fruit and flower, the glands absent; pantropical..... 36. *T. Lappula*

CC. Stamens 5–15; mature fruit (including spines) 4–6 mm. thick.

D. Sepals very slightly cucullate in younger floral buds; fruit very lightly pubescent.

E. Leaves densely tomentose on both surfaces, 9–12 cm. long and 7–10 cm. wide; fruit with few, 50 or less, spines, each about 2 mm. long; Colombia and Ecuador..... 37. *T. sericata*

EE. Leaves lightly pubescent on both surfaces, glabrescent, about 2 cm. long and 1 cm. wide; fruit with numerous, 75–100 short spines, each about 1 mm. long or less; southwestern Mexico..... 38. *T. brachistacantha*

DD. Sepals cucullate about half their length in young floral buds; fruit densely pubescent.

E. Floral buds 5–8 mm. long slightly before anthesis, the urceolus manifest, the stamens 10–15; fruit body densely cinereous-tomentose, the spines glabrescent; West Indies and northern South America..... 39. *T. Bartramia*

EE. Floral buds 3–4 mm. long slightly before anthesis, the urceolus absent, the stamens 5; fruit body and spines densely plumose; northeastern Brazil..... 40. *T. Sampaioi*

AA. Flowers either hermaphrodite or pistillate, the hermaphroditic buds obovoid, the style about twice the length of the ovary; fruits essentially glabrous.
B. Leaves 15–18 cm. long and 16–20 cm. wide, 3- to 5-lobed; stamens 30–40; mature fruit body 5–6 mm. thick, the spines 3–5 mm. long; western Mexico..... 41. *T. paniculata*
BB. Leaves usually 7–15 cm. long and 5–12 cm. wide, not lobed to slightly 3-lobed; stamens 20–30 in hermaphroditic flowers, staminodial or absent in pistillate; mature fruit body 2–4 mm. thick.
C. Pistillate flower apetalous; (hermaphroditic floral bud 5–7 mm. long slightly before anthesis, the petals about 3–4 mm. long); fruit body 3–4 mm. thick, the spines 30–40; southern Mexico..... 42. *T. Galeottiana*
CC. Pistillate flower with petals, each about 1 mm. long; (hermaphroditic flower not seen); mature fruit body about 2 mm. thick, the spines about 20; central Mexico..... 43. *T. heliocarpoides*

16. TRIUMFETTA BREVIPES S. Wats. in Proc. Am. Acad. 22:400. 1887. (T.: *E. Palmer 323*).

Spreading bushy shrubs 1–2 m. high; branches and inflorescence axes rough, scurfy, ferruginous-tomentose. Leaves broadly elliptical, about 11–13 cm. long and 3–4 cm. wide, the base obtuse, the tip gradually acuminate, the serrations unequal and blunt, usually glandular, the upper surface lightly but coarsely stellate-pubescent, the lower densely stellate-tomentose; petioles 1.0–1.5 cm. long, densely tomentose. Inflorescences axillary, the cymes of 2, rarely 3, cymules, generally condensed, the flowering peduncles 3–4 mm. long, the pedicels short, about 2 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 1.0–1.4 cm. long at anthesis, slightly constricted in the middle, the apical appendages slender, about 2–3 mm. long, slightly pubescent; sepals oblong, about 13–16 mm. long including the apical appendages, densely tomentose without, glabrescent within; petals narrowly obovate, about 10 mm. long, the claw about 4 mm. long, shortly plumose; gonophore about 1.5 mm. long and nearly as wide, the glands broadly oblong, 1.0–1.5 mm. long and 0.75–1.0 mm. wide; urceolus large, about 1 mm. high or more, indistinctly lobed, slightly ciliate; stamens 25–30, the filaments smooth, without serrations; ovary orbicular, about 1.5 mm. long, the spinules numerous, recurved, the style about 8–9 mm. long, the stigma acute. Fruit orbicular, the body about 6–7 mm. in diameter at maturity, matted cinereous-tomentose, 3-loculate, each cell 1-seeded, the spines numerous, 100 or more, straight, glabrous, each about 1 mm. long; seeds pyriform, 3.0–3.5 mm. long and 2.5–3.0 mm. wide.

A common ground cover in pine and oak forests or rocky hillsides at altitudes of 1000 m. or more in southwestern Mexico; flowering in August and September, the fruit maturing from late September to mid-October.

MEXICO: GUERRERO: Tierras Blancas, Mina, alt. 1400 m., *Hinton 9922* (GH, US). JALISCO: Río Blanco, *E. Palmer 323* (GH, US); rocky hills under oaks near Guadalajara, *Pringle 4502* (BR, GH, Mo, US); barranca of Río Blanco, near Guadalajara, alt. 4500 ft., *Pringle 11388* (GH, US); near Chapala, *Rose & Painter 7695* (GH, US). MICHOACAN: road from Tancitaro to Apatzingan, alt. 3400 ft., *Leavenworth 1771* (Mo); vicinity of Morelia, Loma Sta. Maria, alt. 1950 m., *Arsène 2516* (K, Mo, P, US); vicinity of Morelia, vers la Huerta, alt. 1950 m., *Arsène 5131* (GH, Mo, US); vicinity of Morelia, alt. 1900 m., *Arsène 5546* (GH, Mo, US).

The shortly petiolate elliptic leaves, the orbicular fruit with numerous very short glabrous spines, and the oblongoid floral bud 10–14 mm. long at about anthesis, are characters which distinguish this species.

17. TRIUMFETTA PALMERI S. Wats. in Proc. Am. Acad. 22:400. 1887. (T.: *E. Palmer 330*).

Low shrubs about 1 m. high; branches and inflorescence axes scurfy, ferruginous-tomentose. Leaves narrowly elliptic, about 6–8 cm. long and 2–3 cm. wide, the base obtuse, the tip gradually acuminate, the serrations rather regular and double, the upper surface lightly stellate-pubescent, the lower more densely so; petioles very short, not longer than 1 cm., densely tomentose, nearly obsolete in the bracts. Inflorescences axillary, the cymes usually of 3 cymules, rarely 4, each cymule 2-, rarely 3-flowered, the flowering peduncles variable in length, usually 4–6 mm. long, the pedicels about 2–3 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 14–18 mm. long slightly before anthesis, usually falcate, the apical appendages short, slender, 1–2 mm. long, slightly pubescent; sepals narrowly ovate, about 15–20 mm. long including the apical appendages, densely tomentose without, glabrescent within; petals about 8–9 mm. long, narrowly obovate, with a claw about 2 mm. long, very densely plumose; gonophore slender, 1.0–1.5 mm. long, the glands oblong, about 1 mm. long and 0.5 mm. wide; urceolus very short, about 0.25 mm. high, rather obscurely 5-lobed, briefly ciliate; stamens 20, the filaments without serrations, slightly pubescent at the base; ovary orbicular, about 1 mm. long, the spinules numerous, recurved, the style 10–12 mm. long, the stigma acute. Fruit orbicular, the body about 4–5 mm. in diameter at maturity, with many short, stellate hairs, 3-loculate, each cell 1-seeded, the spines falcate, about 75, lightly pubescent to retrorsely pilosulose, 2–3 mm. long; seeds pyriform, about 3.0 mm. long and 2.5 mm. wide.

Southwestern Mexico, usually at altitudes of 1000–2000 m.; flowering in mid-August, and the fruit maturing from mid-September to early October.

MEXICO: DURANGO: Sierra Madre, *Rose 3510* (GH). JALISCO: Río Blanco, *E. Palmer 330* (Mo, US); on the road between Colotlán and Bolaños, *Rose 2838* (US); Sierra Madre, west of Bolaños, *Rose 3701* (US); near Guadalajara, *Rose & Painter 7447* (US); barrancas near Guadalajara, *Pringle 4493* (BR, Mo, US); barranca near Río Blanco near Guadalajara, alt. 4500 ft., *Pringle 11389* (US).

This species is closely related to *T. brevipes*, but may be distinguished from the latter by its floral buds, which are 3–4 mm. longer at about anthesis, and also by its falcate, relatively longer, pubescent spines.

18. TRIUMFETTA SOCORRENSIS T. S. Brandg. in Erythea 7:1. 1899. (T.: *Anthony 378*).

Handsome shrubs about 1.5–2.0 m. high; branches and inflorescence axes rough, scurfy, ferruginous-tomentose. Leaves broadly ovate to rhombic-ovate, about 5–6 cm. long and 4–5 cm. wide, the base rounded or cordate, the tip abruptly acuminate, the serrations very irregular, unequal and blunt, the upper surface coarsely stellate-tomentose, the lower more densely so; petioles about 2.0 cm. long, stout,

densely tomentose. Inflorescences axillary, the cymes of 3–4, very rarely 2, cymules, generally condensed, the flowering peduncles very short, 1–2 mm. long, the pedicels 2–3 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, about 9–11 mm. long slightly before anthesis, very slightly constricted near the base, the apical appendages short, about 1 mm. long; sepals broadly elliptical, about 12–13 mm. long at anthesis including the apical appendages, densely tomentose without, glabrescent and greenish within; petals broadly obovate, about 8–9 mm. long, the claw about 2–3 mm. long, densely plumose; gonophore short and stout, about 0.75 mm. long and 1.5 mm. thick, the glands small, spherical; urceolus short, about 0.5 mm. high, distinctly many-lobed, slightly ciliate; stamens about 20, the filaments glabrous; ovary orbicular, about 1.5 mm. long, the spinules about 30, recurved, the style about 3–4 times the length of the ovary, the stigma very briefly 2-fid. Fruit oblongoid, the body about 3–4 mm. in diameter and 5–6 mm. long at maturity, densely stellate-tomentose, 3-loculate, each cell 1-seeded, the spines about 15–20, 6–10 mm. long, densely pubescent with many short spreading hairs; seeds pyriform, 2.0–3.0 mm. long and 1.5–2.0 mm. wide.

Known only from Socorro Island adjacent to the mainland off the coast of Baja California, Mexico; flowering and fruiting from March to June.

MEXICO: REVILLA GIGEDO ISLANDS: I. Socorro: *Anthony 378* (Mo, NY, UC, US); *Barkelew 197* (Mo, UC, US); Grayson's Cove, *Mason 1672* (Mo, US); dry slopes, north anchorage, *Howell 8444* (US).

A very distinct species and an endemic, it is conveniently recognizable by its densely tomentose, rhombic-ovate leaves with very short petioles, and also by its very characteristic oblongoid fruits with few densely plumose, long spines. In its vegetative and floral characters, it is closely related to *T. brevipes*, a common species of southwestern Mexico, and in its fruit characters to *T. Purpusii*, an endemic from Vera Cruz, Mexico.

19. TRIUMFETTA PURPUSII Standl. in Field Mus. Publ. Bot. 11:167. 1936. (T.: *Purpus 9009*).

Tall sparingly branched shrubs about 1.5 m. high; branches and inflorescence axes rough, scurfy, ferruginous-tomentose. Leaves broadly ovate, about 8–9 cm. long and 4–5 cm. wide, the base subcordate, the tip gradually and narrowly acuminate, the serrations unequal and blunt, generally glandular, the upper surface lightly stellate-pubescent, the lower densely tomentose; petioles 3–5 cm. long, densely stellate-pubescent. Inflorescences axillary, the cymes of 2, rarely 3, cymules, generally condensed, the flowering peduncles about 2–3 mm. long, the pedicels of about the same length. Flowers hermaphrodite, the buds broadly oblongoid, 8–12 mm. long slightly before anthesis, the apical appendages very slender, about 6–10 mm. long, usually reflexed upon the bud, densely plumose; sepals oblong, about 16–20 mm. long including the apical appendages, densely long-tomentose without, glabrescent within; petals obovate to narrowly so, about 6–8 mm. long, the claw about 4 mm. long, densely plumose; gonophore about 1.0 mm. long and 1.5–2.0 mm. wide, the glands large, oblong, 1.0–1.5 mm. long and 0.75–1.0 mm. wide;

urceolus small, about 0.5 mm. high, very deeply many-lobed, lightly ciliate; stamens about 40, the filaments smooth; ovary orbicular, about 1 mm. long, the spinules about 50, recurved, the style about 8–9 mm. long, the stigma acute. Fruit suborbicular, the body about 5 mm. wide, very densely tomentose, 3-loculate, each cell 1-seeded, the spines straight, about 40, each about 2 mm. long, with many long plumose hairs; seeds pyriform, 2.0–2.5 mm. long and 1.5–2.0 mm. wide.

Known only from Vera Cruz, Mexico. Flowers and fruits from November to March.

MEXICO: VERA CRUZ: Mata Zarza, *Purpus 9009* (FM, GH, Mo, NY, UC, US); barranca de Panoaya, *Purpus 8609* (GH, Mo, NY, UC, US); Baños de Azufre, *Purpus 8274* (GH, Mo, NY, UC, US); Remudatero, *Purpus 11099* (Mo, US).

The presence of very long appendages of the sepals makes *T. Purpusii* and *T. falcifera* very distinct from the rest of the species. This species can be distinguished from the latter, in flower by its calycine apical appendages, which are not only longer by about 2 mm. or more but are also more densely plumose; and in fruit, by the densely plumose body and the spines.

20. TRIUMFETTA FALCIFERA Rose, in Contr. U. S. Nat. Herb. 12:285. 1909. (T.: *E. Palmer 63*).

Bushy shrubs about 2 m. high; branches and inflorescence axes smooth with many long, spreading, stellate hairs. Leaves narrowly to broadly ovate, 12–15 cm. long and 6–9 cm. wide, the base obtuse to subcordate, the tip narrowly and gradually acuminate, the serrations rather regular, generally glandular, the upper surface lightly stellate-pubescent, the lower more densely and softly so; petioles 5–7 cm. long with long, spreading, stellate tomentum. Inflorescences generally axillary, sometimes terminal, the cymes of 1 cymule, the flowering peduncles about 8 mm. long and the pedicels about 6 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 6–10 mm. long at anthesis, the apical appendages very slender, 5–7 mm. long, usually spreading, rather densely plumose; sepals oblong, about 12–16 mm. long including the apical appendages, lightly long-plumose without, brownish and glabrescent within; petals obovate, about 3–4 mm. long, the claw about 1 mm. long, lightly plumose; gonophore about 1 mm. long, nearly 2 mm. wide, the glands narrowly elliptical; urceolus rather short, 0.25–0.5 mm. high, distinctly many-lobed, lightly ciliate; stamens about 40, the filaments glabrous; ovary orbicular, about 1.5 mm. long, the spinules about 40, recurved, the style 6–7 mm. long, the stigma acute, sometimes very briefly 2-fid. Fruit orbicular, about 4 mm. in diameter at maturity, very lightly pubescent, usually 3-loculate, sometimes 4- to 6-celled by false-septation, each cell 1-seeded, the spines about 40, straight, essentially glabrous, each about 2 mm. long; seeds pyriform, 2.0–2.5 mm. long and 1.5–2.0 mm. wide.

Southern Mexico; flowering and fruiting in September and October.

MEXICO: GUERRERO: in Acapulco and vicinity, *E. Palmer 63* (US), *266* (Mo, UC, US); Baqueta, alt. 200 m., *Langlassé 502* (P, US); Acapulco, presqu'iles Griffon, *Le Jolis s. n.* (G). TABASCO: Jalapa, Tequisatlán, *Liebmann 502* (US). DATA INCOMPLETE: *Liebmann 534A* (US).

21. TRIUMFETTA MULTILOCULARIS Hochr. in Ann. Conserv. Jard. Bot. Genève 18:104. 1914. (T.: *Pavon s. n.* in Herb. Genève).

Small trees or shrubs 2–4 m. high; branches and inflorescence axes rough, rather densely tomentose, with relatively long, ferruginous, stellate hairs. Leaves broadly ovate, usually 3-lobed, 8–10 cm. long and 6–7 cm. wide, cordate, narrowly and gradually acuminate, the serrations very irregular and rather large, not glandular, the upper surface coarsely stellate-pubescent, the lower more softly and densely so; petioles 4–6 cm. long, rather stout, with many spreading, long, stellate hairs. Inflorescences axillary, the cymes usually of 1, rarely 2, cymules, loose and spreading, the bracts usually broadly ovate, not lobed, the flowering peduncles 8–12 mm. long, the pedicels about 6 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 22–25 mm. long and 3–4 mm. wide slightly before anthesis, the apical appendages rather stout, 2–3 mm. long, lightly pubescent; sepals broadly obovate, about 27 mm. long including the apical appendages, stellate-pubescent without, glabrescent within; petals broadly obovate, showy, about 24 mm. long and 4–6 mm. wide, the claw about 4 mm. long, densely plumose; gonophore large, about 1.5–2.0 mm. long and wide, the glands quadrangular, large, about 1.5 mm. long and 1.0 mm. wide; urceolus 10-lobed, about 0.75 mm. high, distinctly ciliate; stamens 25–30, the filaments retrorsely 2-serrate, slightly pubescent at the base; ovary ovoid, 1.5–2.0 mm. long, the spines numerous, recurved, the style about 22 mm. long, pubescent at the base, the stigma acute. Fruit orbicular, the body about 6–8 mm. in diameter at maturity, lightly and briefly stellate-pubescent, 3- to 5-loculate, each cell 2-seeded, later falsely 8- to 10-loculate, each cell with 1 seed, the spines numerous, short, 1–2 mm. long, very shortly pubescent; seeds ovoid, about 2 mm. long and broad.

Peru; growing at altitudes of 2000–3000 m.; flowering and fruiting from June to December.

PERU: AYACUCHO: between Huanata and Río Apurimac, alt. 2200 m., *Killip & Smith 22309* (US). CUZCO: San Miguel, Urubamba Valley, alt. 1800 m., *Cook & Gilbert 1126, 1163* (US); Prov. Quispicanchis, Dist. Marcapata, *Vargas 9685* (Mo); below Machu Picchu, lower valley slopes, alt. 2100 m., *West 6473* (Mo). HUANUCO: "Fl. de Huayaquil", *Pavon s. n.* (G); "Herbier de Ventenat", *s. n.* (G, FM photo); Acomayo, upon banks of Río Acomayo, alt. 2100 m., *Woytkowski 34013* (Mo). JUNIN: Prov. Tarma, Carpapata, alt. 2400 m., *Ochoa 287* (US); Carpapata, above Huacapistana, alt. 2400 m., *Killip & Smith 24361* (US); Huacapistana, *Rose & Rose 18550* (NY, US); Prov. Tarma, between Palca and Carpapata, alt. 2900 m., *Stork 10970* (Mo). LIMA: Escuela Nac'l. Agric., from Prov. Sandia & Huacapistana and Tarma, *Mexia 4065* (Mo). DATA INCOMPLETE: Amazonian slope of the Andes, alt. 10,000–11,000 ft., *B. Eble s. n.* (NY).

Ornamental shrub or small tree with long whip-like branches. Though sufficiently distinct from *T. mollissima*, it is usually misidentified with it. The much larger flowers with broadly obovate, rather showy petals, and the pubescent to nearly glabrescent fruits, with numerous very short spines, clearly distinguish this species from the former.

22. TRIUMFETTA MOLLISSIMA HBK. Nov. Gen. & Sp. 5:345. 1821. (T.: "S. Fé de Bogota," *Bonpland s. n.* in Herb. Paris.).

Triumfetta acuminata HBK. loc. cit. 344. 1821. (T.: *Bonpland s. n.* in Herb. Paris.).

Shrubs about 1–2 m. high; branches and inflorescence axes rough, very densely long ferruginous-tomentose. Leaves broadly ovate to 3-lobed, 12–15 cm. long and 6–8 cm. wide, rounded or subcordate at the base, gradually and narrowly acuminate, the serrations very irregular, blunt and generally glandular, the upper surface scabrous, very pubescent, the lower smooth, densely tomentose; petioles 3–5 cm. long, rather stout, with long spreading ferruginous tomentum. Inflorescences axillary, the cymes of 2–3, rarely 1, cymules, rather lax, the bracts broadly lanceolate to elliptical, long-acuminate, the flowering peduncles about 8 mm. long, the pedicels about 6 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 15–20 mm. long and about 2 mm. wide slightly before anthesis, the apical appendages slender, 1–2 mm. long, very lightly pubescent; sepals narrowly elliptical, 18–22 mm. long at anthesis, with many long spreading stellate hairs without, glabrescent within; petals linear, 16–18 mm. long, the claw 3–4 mm. long, densely plumose; gonophore rather large, about 1 mm. long and 1–2 mm. wide, the glands quadrangular, large, subequalling the gonophore; urceolus about 1 mm. high, distinctly 5-lobed, densely ciliate; stamens 20, the filaments slightly pubescent at the base, smooth; ovary orbicular, about 2 mm. long, the spinules numerous, recurved, the style 16–17 mm. long, the stigma acute. Fruit orbicular, the body 6–8 mm. in diameter at maturity, densely tomentose with long spreading hairs, 4-loculate, each cell 2-seeded, later falsely 8-loculate with 1 seed to a cell, the spines numerous, 100 or more, each 2–3 mm. long, long-plumose at the base; seeds ovoid, about 2 mm. long and broad.

Known only from Colombia; growing in dry open areas, at altitudes of 1200–2000 m.; flowering and fruiting from May to November.

COLOMBIA: ANTIOQUIA: vic. Medellin, *Toro 117, 501, 701* (NY); Dabeiba, *Johnson & Barkley 18c 676* (US); Bello, alt. 1500–1800 m., *Archer 218* (US). CALDAS: Supia, Cordillera Occidental, alt. 1200–1500 m., *Pennell 10710* (NY). CAUCA: forests in highlands of Popayán, alt. 1700–2000 m., *Lehmann 5521* (NY, US); Tolima, *Lehmann 2196* (G); Río Sucio to Río Piedras, west of Popayán, alt. 1500–1700 m., *Pennell & Killip 8227* (NY); La Manuelita, near Palmira, eastern side of Cauca Valley, alt. 1100–1300 m., *Pittier 818* (US); Municipio Popayán, alt. 1800 m., *Agredo 252* (US); El Tambo, Vertiente Oriental, alt. 1700 m., *Sneidern 4745, 5559, 5671* (US); Popayán, matorrales en Río Blanco, alt. 1800 m., *Arbelaez & Cuatrecasas 5761* (US); El Tambo, *Garcia B. 4418* (US). CUNDINAMARCA: Estacion Santana, arriba de Sasaima, alt. 1600–1700 m., *Dugand & Jaramillo 3845* (US); entre Pandi e Icononzo, alt. 980–1340 m., *Garcia B. 11995* (US); Villete, *Ariste-Joseph s. n., 5373* (US). DISTRITO FEDERAL: S. Fé de Bogota, *Bonpland s. n.* (P, Mo photo, NY); exact locality lacking, *Bonpland s. n.* (P, Mo photo). VALLE: Palmira, Cordillera Central, alt. 1200–1800 m., *Pennell & Killip 6101* (NY); Pichinde, bank of Río Cali, alt. 1600 m., *Duque 1474* (US); La Cumbre, Cordillera Occidental, alt. 1500–1700 m., *Pennell 5214* (US); Río Bolo, alt. 1000 m., *Dryander 253, 254* (US). DATA INCOMPLETE: *Triana 3230* (US); *Mutis 2788, 4171* (US); Piedra de Moler, *Holton 778* (NY); *Linden s. n.* (NY).

The reason for the discrepancy in the description of the leaf-shape of *T. acuminata* is very obviously due to the fact that the authors mistook the bracts for vegetative leaves. I have seen the types of both *T. mollissima* and *T. acuminata* and am convinced that they are conspecific. The type of *T. mollissima* has both the vegetative leaves and the bracts, while that of *T. acuminata* has only the bracts.

23. TRIUMFETTA LONGICOMA St. Hil. Fl. Bras. Merid. 1:221. 1825. (T.: *St. Hilaire B. 19*).

Older branches smooth, glabrescent, the younger ones and inflorescence axes longitudinally ridged, clothed with long stellate hairs. Leaves broadly ovate, about 8 cm. long and 4–6 cm. wide, cordate, narrowly and gradually long-acuminate, both surfaces with scattered tufts of long stellate hairs, especially on the veins; petioles 2–3 cm. long, slender, with few long stellate hairs. Inflorescences axillary, the cymes of 2–3 cymules, the flowering peduncles 3–4 mm. long, the pedicels 2–3 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, about 15 mm. long and 2–3 mm. wide slightly before anthesis, the apical appendages short, about 1 mm. long, glabrescent; sepals oblong, about 17 mm. long, densely pubescent without with long stellate hairs, glabrescent within; petals obovate, about 14 mm. long and 3 mm. wide, the claw about 2–3 mm. long, briefly ciliate; gonophore stout, about 1.0 mm. long and 1.5 mm. wide, the glands narrowly elliptical; urceolus deeply 5-lobed, about 0.5 mm. high, densely ciliate; stamens about 20, the filaments smooth, glabrous; ovary ovoid, about 1 mm. long, the spinules numerous, recurved, the style about 10 mm. long, the stigma acute. Fruit lightly stellate-pubescent, the body about 5 mm. in diameter at maturity, 3-loculate, each cell 2-seeded, later 6-celled each with 1 seed by false septation, the spines numerous, slender, each about 4 mm. long, lightly pubescent; seeds ovoid, about 2 mm. long and broad.

Apparently a rare species of northeastern Brazil, usually growing along streambanks in wooded areas at altitudes of about 1000 m.; flowering and fruiting from May to July.

BRAZIL: MINAS GERAIS: Cobras, *St. Hilaire B. 19* (P, FM photo, US); Distr. Diamantina, Christais, near Corriga Duas Pontes, alt. 1160 m., *Mexia 5821* (NY, US). DATA INCOMPLETE: *Allemao & Sysneiros 1491* (R).

The characters that help in the identification of this species are the long golden-brown silky stellate tomentum, which clothes the younger branches, the inflorescence axes, the outside of the sepals, the leaves and the petioles, the relatively large flowers, and the comparatively long but weak spines. It is quite likely that *T. longicoma* is conspecific with the Old World *T. velutina* Vahl. I have not seen the type of the latter, but have seen a specimen from India in Hooker's Herbarium at Kew, labelled *T. velutina*, which matches well *T. longicoma*.

24. TRIUMFETTA CHIHUAHUENSIS Standl. in Contr. U. S. Nat. Herb. 23:744. 1923. (T.: *M. E. Jones s. n.* in U. S. Nat. Herb.).

Slender spreading shrubs 1–2 m. high; older branches lightly pubescent to

Fig. 8. *Triumfetta chihuahuensis*

nearly glabrate, punctate with prominent white lenticels, the younger stems and inflorescence axes densely pubescent with short stellate and simple hairs. Leaves broadly ovate, generally 3-lobed, 11–14 cm. long and 6–9 cm. wide, distinctly cordate, the middle lobes narrowly and gradually acuminate, the laterals acute to shortly acuminate, both surfaces nearly glabrous, only the primary veins lightly pubescent; petioles slender, 6–7 cm. long, briefly stellate-pubescent. Inflorescences axillary, the cymes of 2–3 cymules, usually opposite the bracts, the flowering peduncles about 5 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, showy, the buds broadly oblongoid, 24–26 mm. long and 3–4 mm. wide slightly before anthesis, the apical appendages about 1 mm. long, glabrescent; sepals oblong, 25–30 mm. long including the apical appendages, scattered stellate-pubescent without, glabrescent within; petals broadly obovate, 20–22 mm. long and 4–5 mm. wide, the claw about 3–5 mm. long, densely but very briefly pubescent; gonophore large, about 2.5 mm. long and 1.5 mm. wide, the glands oblong, about 2 mm. long and 1 mm. wide; urceolus short, distinctly many-lobed, briefly ciliate; stamens 20, the filaments smooth, lightly stellate-pubescent at the base; ovary orbicular, about 2 mm. long, the spinules numerous, recurved, the style about 22 mm. long, the stigma very briefly 3-parted. Fruit orbicular, the body about 6 mm. in diameter at maturity, very lightly stellate-pubescent, 3-loculate, each cell 1-seeded, the gonophore and glands prominent, the spines about 75–100, lightly pubescent with few scattered hairs; seeds ovoid, about 3.5 mm. long and 3.0 mm. wide.

Known only from southwestern Mexico, where it grows along steep, moist, shady canyons in pine forests at altitudes of 1000–1500 m.; flowers and fruits in September and October.

MEXICO: CHIHUAHUA: Guayanopa Canyon, Sierra Madre Mts., alt. 5000 ft., *M. E. Jones s. n.* (Mo, US); near Batopilas, alt. 5500–6500 ft., *Goldman 211* (GH, US); Arroyo Hondo, Sierra Charuco, *Gentry 1780* (Mo, US). SINALOA: Ocurahui, Sierra Surotato, alt. 6000–7000 ft., *Gentry 6240* (Mo). SONORA: Sanguaribo, Río Mayo, alt. 5500 ft., *Gentry 2123* (Mo, US).

This species is rather closely related to *T. columnaris*, but may be distinguished from it by the larger, usually 3-lobed leaves and also by the pubescent spines.

25. TRIUMFETTA **barbosa** Ko Ko Lay, sp. nov.

Frutex circiter 2–4 m. altus. Ramuli graciles longitudinaliter sulcati 4-angulati glabrescentes. Folia late ovata non-lobata 14–16 cm. longa 7–10 cm. lata base cuneata vel rotundata apice longe attenuata subdupliciter serrata pilis sparse stellatis mox glabrescentia infra breviter stellato-pubescentia, in axillis nervorum dense longi-pubescentia. Inflorescentiae axillares, cymis cymulis 2, pedunculis circiter 4 mm. longis, pedicellis 8–10 mm. longis. Flores hermaphroditi, alabastro maturo oblongoideo 18–20 mm. longo; sepalis ellipticis 20–22 mm. longis extra breviter pubescentibus, appendiculis circiter 2 mm. longis glabris; petalis ellipticis vel obovatis 14–16 mm. longis, unguilo 2–3 mm. longo dense plumoso; gonophoro circiter 1.5 mm. longo, glandulis ellipticis 0.75–1.0 mm. longis; urceolo circiter 0.75 mm. alto, 5-lobato breviter ciliato; staminibus 20, filamentis usque ad 12–14

Fig. 9. *Triumfetta barbosa*

mm. longis glabris; ovario globoso circiter 1.5 mm. longo, spinulis 75–100 recurvatis, stylo glabro 15–16 mm. longo, stigmate acuto. Fructus globosus non dehiscens, corpore ipso 4–6 mm. diametro, breviter stellato-pubescens 3-locularis, loculis 1-spermis, aculeis circiter 75, 3–4 mm. longis breviter pubescentibus; seminibus ovoideo-acutis circiter 2 mm. longis et latis.

West-central Mexico.

Mexico: Jalisco: Sierra Madre Occidental, Real Alto, trail to Arroyo del Jaguay, alt. 2500 m., *Mexia 1753* (holotype in Herb. Mo. Bot. Gard.; isotypes in Herb. Univ. Mich. and U. S. Nat. Herb.).

A species rather closely allied to *T. chihuahuensis*, but may be distinguished by its undivided long-attenuate leaves with dense tufts of hairs in the axils of the veins on the lower surface, and also by its more densely pubescent spines and glabrous filaments.

26. Triumfetta columnaris Hochr. in Ann. Conserv. Jard. Bot. Genève 18:111. 1914. (T.: *Hartweg 448*).

Triumfetta pseudocolumnaris Hochr. loc. cit. 103. 1914. (T.: *Galeotti 4151*).
Triumfetta columnarioides Bullock, in Kew Bull. 292. 1937. (T.: *Hinton 4917*).

Shrubs about 2 m. high; older branches glabrescent, longitudinally ridged, the younger ones and inflorescence axes scurfy, with long spreading stellate and simple hairs. Leaves broadly ovate to obscurely 3-lobed, usually small, 6–8 cm. long and 3–4 cm. wide, rounded or subcordate at the base, gradually and narrowly long-acuminate, both surfaces lightly stellate-pubescent, slightly more so on the veins; petioles relatively stout, about 2–3 mm. long, coarsely long stellate-pubescent. Inflorescences axillary, the cymes of 2 cymules, usually opposite the bracts, the flowering peduncles 4–6 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 22–25 mm. long and about 3 mm. wide slightly before anthesis, the apical appendages slender, 1–2 mm. long, glabrescent; sepals oblong, about 25 mm. long including the apical appendages, glabrescent and brownish without, light yellow within; petals narrowly obovate, about 18 mm. long and 3–4 mm. wide, the claw 4–5 mm. wide, densely but briefly ciliate; gonophore large, about 2 mm. long and 1 mm. wide, the glands oblong; urceolus about 0.5 mm. high, 5-lobed, briefly ciliate; stamens 20, the filaments smooth, long stellate-pubescent at the base; ovary orbicular, about 2 mm. long, the spines numerous, recurved, the stigma very briefly 3-parted. Fruit orbicular, the body about 6 mm. in diameter at maturity, lightly stellate-pubescent, 3-loculate, each 1-seeded, the spines about 75–100, each 1–2 mm. long, lightly pubescent to nearly glabrate, the gonophore and glands prominent; seeds ovoid, about 2.5 mm. long and 1.5–2.0 mm. wide.

Central and southwestern Mexico, usually growing in oak forests, at altitudes of 1500–2500 m.; flowering and fruiting from October to December.

Mexico: Guerrero: Mina, Fresnos, alt. 2160 m., *Hinton 9749* (GH, US); Río Frio Diamentes, Mina, *Hinton 10734* (GH, Mo, US). México: Comunidad, Temascaltépec, alt. 2350 m., *Hinton 4891* (GH, K, Mo, US), alt. 2300 m., *4917* (Mo, US). Michoacan: Sierra Terricillia, Coalcomán, alt. 2420 m., *Hinton 12349, 15144, 15270* (GH). Morelos: Cuernavaca, *Holway 532* (NY). Oaxaca: Cordillera, alt. 5000–6000 ped., *Galeotti 4151* (BR, FM photo); Tokontepeque (Tehuantepec?), *Hartweg 448* (NY, FM photo); "les montagnes ombragier en terre tempiric," *Ghiesbreght 175* (P).

The small leaves and large flowers tend to confuse this species with *T. Goldmani*, when examined superficially.

27. TRIUMFETTA GRANDIFLORA Vahl, Eclog. Amer. 2:34. 1796. (T.: *Ryan s. n.* in Herb. Copenhagen).

Triumfetta nemoralis St. Hil. Fl. Bras. Merid. 1:221. 1825. (T.: *St. Hilaire B. 1. 1070* in Herb, Paris.).
Triumfetta longiseta DC. Pl. Rar. Jard. Genève, 64. 1829. (T.: *Burat s. n.* "Havanne" in Herb. Deless.).
Triumfetta longicuspis Turcz. in Bull. Soc. Nat. Moscou 31[1]:229. 1858. (T.: *Jörgensen 882*).
Triumfetta cymosa Tr. & Planch. in Ann. Sci. Nat. Bot. IV, 17:353. 1862. (T.: "Quindio," *Triana s. n.* in Herb. Paris.).
Triumfetta cymosa var. *glabrescens* Tr. & Planch. loc. cit. 354. 1862.
Triumfetta cymosa var. *hirsuta* Tr. & Planch. loc. cit. 354. 1862. (T.: "Pampalona," *Triana s. n.* in Herb. Paris.).
Triumfetta grandiflora var. *brasiliensis* Hochr. in Ann. Conserv. Jard. Bot. Genève 18:100. 1914. (T.: *Glaziou 9356*).
Triumfetta boyacana Moldenke, in Phytologia 1:10. 1933. (T.: *Lawrance 7*).
Triumfetta Schunkei Macbr. in Candollea 5:381. 1934. (T.: *Schunke 1597*).

Shrubs 1–2 m. high; older branches glabrous, smooth, punctate with small white lenticels, the younger stems and inflorescence axes rough, generally clothed with many long stellate and simple hairs. Leaves broadly ovate, usually about 14 cm. long and 9 cm. wide, sometimes slightly larger, rounded or cuneate at the base, narrowly and gradually long-acuminate, both surfaces glabrescent or lightly scabrous with short stellate hairs, especially on the nerves; petioles slender, about 6–10 cm. long, usually lightly stellate-pubescent. Inflorescences terminal, the cymes of 1–2 cymules, usually opposite the bracts, the flowering peduncles about 6 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 14–18 mm. long and 3–4 mm. wide slightly before anthesis, the apical appendages slender, 1–2 mm. long, glabrescent; sepals linear-ovate, 15–20 mm. long including the apical appendages, glabrescent or lightly ferruginous-pubescent without; petals lanc ate to narrowly obovate, subequalling the sepals, the claw 3–5 mm. long, densely plumose; gonophore about 1.5 mm. long and 2.0 mm. wide, the glands spherical; urceolus about 0.5 mm. high, many-lobed, briefly ciliate; stamens 20, the filaments glabrous, smooth; ovary orbicular, about 2 mm. long, the spinules numerous, recurved, the style 14–16 mm. long, the stigma very briefly 3-parted. Fruit lightly pubescent, the body 5–6 mm. in diameter at maturity, rather easily loculicidally dehiscent, 3-loculate, each cell 2-seeded, the spines numerous, about 200, slender, 4–5 mm. long, lightly pubescent at the base, sometimes with few plumose hairs; seeds pyriform, glabrous, about 2–3 mm. long and 1.5–2.5 mm. wide.

Rather widely distributed throughout the American tropics, though not abundant at any single locality, usually growing at altitudes of about 1000 m.; flowering and fruiting in its northern range from September to December, and in its southern range from March to June.

MEXICO: OAXACA: Sierra San Pedro Nolasco, Talea, *Jörgensen 882, 960* (G); Chinantla, *Galeotti 4162A* (BR, NY, US). VERA CRUZ: Sierra Madre Misantla, *Purpus 6009* (UC).
GUATEMALA: ALTA VERAPAZ: Coban, alt. 1350 m., *Tuerckheim II 861* (BR, GH, Mo), alt. 4300 pp., *Tuerckheim 342* GH).

PANAMA: CHIRIQUÍ: vicinity of El Valle de Antón, *Allen 2072* (Mo).
CUBA: HAVANA: près de la Havana, *M. Santos-Burat s. n.* (P, Mo photo).
MARTINIQUE: *Sieber 79* (Mo); *Duss 2318* (Mo, NY).
COLOMBIA: BOYACA: region of Mt. Chapon, northwest of Bogotá, *Lawrance 7* (NY, US). SANTANDER: Eastern Cordillera, between El Roble and Tona, *Killip & Smith 19399* (US).
BRAZIL: MINAS GERAIS: Ponte dos Paulistas, Comarca do Cerro do Frio, *St. Hilaire B. I. 1070* (P); Belo Horizonte, *Barreto 7923* (R). RIO DE JANEIRO: Serra de Estrella près de Botequin, *Glaziou 9356* (BR, G); environs de Rio de Janeiro, *Glaziou 17470* (G). DATA INCOMPLETE: *Ryan s. n.* (C, FM photo).
ECUADOR: PICHINCHA: Puente Gloria de María, west of Quito, alt. 1200 m., *Asplund 7250* (US).
PERU: JUNIN: Chanchamayo Valley, alt. 1500 m., *Schunke 1597* (FM). PUNO: Sandia, alt. 2100–2300 m., *Weberbauer 507, 508* (G). DATA INCOMPLETE: *Poeppig 2053* (FM photo).
BOLIVIA: COCHABAMBA: Incachaca-S. Antonio, alt. 1500 m., *Werdermann 2127* (Mo). LA PAZ: Prov. South Yungas, Bassin Río Bopi, San Bartolomé, near Calisaya, alt. 750–900 m., *Krukoff 10246* (Mo); Mapiri, *Bang 1499* (Mo, US); Achiquin, between Mapiri and Apolo, alt. 750 m., *Cardenas 1110* (NY); San Carlos, Mapiri, *Buchtien 1823* (US). TIPUANI: Hacienda Casana, *Buchtien 7368* (US).

The best single character for the identification of this species is its fruits, which are usually rather easily dehiscent at maturity and have numerous, very long slender spines. In flower, it may be recognized by its broadly oblongoid floral buds, which are about 14–18 mm. long and 3 mm. wide at about anthesis. The leaves are broadly ovate and the base is never cordate. There is considerable variation in the pubescence of the leaves; in general, though not always, plants from South America tend to be more pubescent than those from North America.

28. TRIUMFETTA DISCOLOR Rose, in Contr. U. S. Nat. Herb. 12:285. 1909. (T.: *Rose 1979*).

Triumfetta dehiscens Rose, loc. cit. 285. 1909. (T.: *Rose 1698*).

Low, spreading, bushy shrubs about 8 dm. high; branches and inflorescence axes rough, scurfy, with many long, spreading, stellate hairs. Leaves broadly ovate to rhombic-ovate, about 7–9 cm. long and 6–8 cm. wide, the base rounded, rarely subcordate, the tip abruptly acute, the serrations unequal, blunt and irregular, the upper surface greenish, with few scattered, short, coarse, stellate hairs, the lower pallid, smooth, with dense stellate tomentum; petioles 3–5 cm. long, clothed with long, spreading, stellate hairs. Inflorescences axillary, rarely terminal, the cymes of 2 cymules, rather lax, the flowering peduncles 3–4 mm. long, the pedicels about 2 mm. long, the subtending bracteoles prominent. Flowers hermaphrodite, the buds oblongoid, about 15–20 mm. long slightly before anthesis, the apical appendages short, about 1 mm. long, lightly pubescent; sepals oblong, about 18 mm. long, brownish and lightly pubescent without, greenish and glabrescent within; petals broadly obovate, about 15 mm. long and 3–4 mm. wide, deep yellow, the claw about 2–3 mm. long, slightly plumose; gonophore broad, about 1 mm. long and 2–3 mm. wide, the glands quadrangular, subequalling the gono-

phore; urceolus prominent, about 0.75 mm. high, many-lobed, densely ciliate; stamens usually 20, rarely 25, the filaments glabrous; ovary orbicular, about 2 mm. long, the spinules numerous, recurved, the style 15–17 mm. long, the stigma acute. Fruit orbicular, the body about 6–7 mm. in diameter at maturity, slightly stellate-pubescent, loculicidally dehiscent, 3-loculate, each cell 2-seeded; spines about 75, about 2 mm. long, lightly pubescent; seeds ovoid, about 1.5–2.0 mm. long and 1.0–1.5 mm. wide.

Western Mexico, usually growing on rocky shaded slopes under oaks or in oak-savannahs at altitudes of 1000–1700 m.; flowering and fruiting from July to September.

MEXICO: DURANGO: Huasemote, *Rose & Hough 3503* (GH, US); along trail from Pueblo Nuevo to Cueva, Sierra Madre Occidental, alt. 1500–1700 m., *Harvey 18486* (US); exact locality lacking, *Rose 2255* (US). JALISCO: in the foothills of Sierra Madre, near Colomos, *Rose 1698* (GH, US). NAYARIT: in the foothills of Sierra Madre, Terr. de Tépic, between Pedro Paulo and San Blascito, *Rose 1979* (GH). SINALOA: Cerro Colorado, alt. 2500 ft., *Gentry 5127* (GH, Mo); Las Mesas, Sierra Surotato, alt. 3000 ft., *Gentry 6150* (GH, Mo), *6151* (Mo, US), *6151a* (Mo); Quebrado de Mansana, Sierra Surotato, alt. 4000–4500 ft., *Gentry 6526a* (GH, Mo); Las Mesas, Sierra Surotato, alt. 3000 ft., *Gentry 6652* (GH, Mo). SONORA: Sierra de Alamos, vicinity of Alamos, *Rose, Standley & Russell 12881* (NY, US).

The lightly stellate, easily dehiscent fruits, the large showy flowers, and the rhombic-ovate leaves with dense tomentum on lower surfaces, characterize this species.

29. TRIUMFETTA ABUTILOIDES St. Hil. Fl. Bras. Merid. 1:223. 1825. (T.: *St. Hilaire s. n.*, "Itajuru de San Miguel de Mato Dentro" in Herb. Paris.).

Sparsely branched, more or less trailing shrubs 1–3 m. high; older branches terete, scurfy, rather densely pubescent with long stellate and simple, frequently gland-tipped hairs, the younger ones and inflorescence axes very densely tomentose with long, spreading, stellate and simple hairs. Leaves broadly ovate, markedly 3-lobate, the lobes usually above the middle of the lamina, 12–14 cm. long and 8–10 cm. wide, the base subcordate, the terminal lobe long-acuminate, the laterals usually blunt, very rarely short-acuminate, the serrations very irregular, the basal ones always glandular, both surfaces densely pubescent with both stellate and simple hairs, the veins densely tomentose, the lower ones very prominent; petioles 3–4 mm. long, stout, densely long-tomentose, usually flattened and forming a callus at the sinus. Inflorescences on terminal branches, the cymes of 3 cymules, always in the axils of the bracts, rather lax, the bracts elliptical, the flowering peduncles about 3 mm. long, the pedicels 3–4 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, about 8–11 mm. long slightly before anthesis, the apical appendages about 1 mm. long; sepals oblong, 8–11 mm. long, grayish and rather densely tomentose without, yellow-brown and glabrescent within; petals subequalling the sepals, broadly obovate, showy, 7–10 mm. long and about 3 mm. wide, the claw 2–3 mm. long, densely plumose; gonophore slender, about 0.5 mm. long, the glands spherical to oblong, subequalling the gonophore; urceolus short,

about 0.5 mm. high, distinctly 5-lobed, densely ciliate; stamens 20, the filaments retrorsely 4-serrate; ovary orbicular, about 1.5 mm. high, the spinules numerous, recurved, the style 5–6 mm. long, the stigma briefly 3-parted. Fruit spheroid, the body rather densely pubescent, 3–5 mm. in diameter at maturity, 3-loculate, each cell with 2 seeds, on maturity with 6 definite 1-seeded locules, the spines 100 or more, each about 3 mm. long, retrorsely pilosulose; seeds lenticular, about 2 mm. long and wide, the funicular groove prominent.

A rather common widespread species of South America, with a few scattered representatives in the West Indies; commonly found in abandoned fields or as a roadside weed at altitudes from about 300 to 1500 m.; flowers and fruits from January to April.

HAITI: Massif de la Selle, Port-au-Prince, alt. 300 m., *Ekman 7213* (S), *7407* (S). COLOMBIA: CAUCA: Las Suntas, alt. 300–500 m., *Lehmann 234* (G). MAGDALENA: Santa Marta, *H. H. Smith 1689* (NY, US).

VENEZUELA: DISTRITO FEDERAL: in valley, on road from El Valle to Cua, *Pittier 11974* (G); between Cotiza and Los Venados, near Caracas, *Allart 21* (US); Caracas and vicinity, *Bailey & Bailey 257* (US).

BRAZIL: MINAS GERAIS: Caldas, *Regnell I. 102* (S, US); Dist. Carangola, Fazenda da Gramma, about 6 km. north, *Mexia 4324* (Mo, US); Caldas, in campo, *Lindberg 284b* (BR, S); Itajuru de San Miguel de Mato Dentro, *St. Hilaire s. n.* (P); Passa Quatro, *Sampaio 6033, 6118* (R); Domingos Pisoni, Municipio de Leopoldini, *Barreto 7928* (R); Jard. Bot. de Belo Horizonte, *Barreto 7922* (R); exact locality lacking, *Claussen 482* (BR). RIO DE JANEIRO: Nova Friburgo, alt. 900 m., *Holway & Holway 1459* (US). RIO GRANDE DO SUL: Tristeza, Porto Alegro, *Malme 1494* (S); Canôas, Prov. Porto Alegro, *Malme s. n.* (S); Cascate, Prov. Gloria, *Malme 1353* (S). SÃO PAULO: Carapicho, *Mosén 1132* (S). SANTA CATHARINA: *Ule 813* (US). DATÁ INCOMPLETE: *Burchell 2491* (P).

ECUADOR: GUAYAS: Milagro, alt. 500 m., *Hitchcock 19960, 20240* (US). MANABI: Portoviejo, *Rose & Rose 23409* (US).

PERU: CUZCO: Prov. Quispicanchis, Tio, Marcapata, alt. 2000 m., *Vargas C. 3079* (Mo); Torontoy, Urubamba Valley, alt. 2400 m., *Cook & Gilbert 819* (US); Santa Ana, alt. 900 m., *Cook & Gilbert 1437* (US). HUANUCO: Huanuco, *Macbride 3521* (US); *Macbride & Featherstone 2053* (US). LORETO: Mishuyacu, near Iquitos, alt. 1000 m., *Killip & Smith 29894* (US). DATA INCOMPLETE: *Grisar s. n.* (P).

BOLIVIA: LA PAZ: Mapiri, alt. 2500 ft., *Rusby 1450* (US); Hacienda Simao sobre el camino a Tipuani, alt. 1400 m., *Buchtien 5452* (Mo, S, US), *5453, 5454* (US); Caranaim, Tipuani, *Buchtien 7367* (S, US); Nord Yungas, Milluguaya, alt. 1300 m., *Buchtien 788* (FM, Mo, S, US); Sirupaya bei Yanacachi, alt. 2100 m., *Buchtien 509* (US), *510* (S); Villa Aspiazu, *Holway & Holway 688* (US).

PARAGUAY: L'Asuncion, *Balansa 2327* (P).

ARGENTINA: FORMOSA: Riocho de Oro, *Reales s. n.* (Mo). MISIONES: Candelaria, Santa Ana, *Schwindt 49* (Mo); Posadas, *Ekman 199* (S, US). TUCUMÁN: Tafi, alt. 600 m., *Venturi 1767* (US).

This species is very closely related to *T. bogotensis*, with which it is often confused. It may, however, conveniently be distinguished from the latter by the very densely pubescent leaves, the short apical appendages of the sepals, and also by the presence of false septa in the fruit, which on maturity becomes completely 6-loculate, each with one seed.

30. TRIUMFETTA BOGOTENSIS DC. Prod. 1:506. 1824. (Based on *T. pilosa* HBK.).

Triumfetta pilosa HBK. Nov. Gen. & Sp. 5:343. 1821, non Roth (T.: *Bonpland s. n.* in Herb. Paris.).

Triumfetta sepium St. Hil. Fl. Bras. Merid. 1:22. 1825. (T.: *St. Hilaire Al. 156*).
Triumfetta dumetorum Schlecht. in Linnaea 11:377. 1837. (T.: *Keerl s. n.* in Herb. Brux.).
Triumfetta hispida A. Rich. in Sagra, Hist. Nat. Cuba 10:204. 1839. (T.: *de la Sagra s. n.* in Herb. Paris.).
Triumfetta grossulariaefolia A. Rich. loc. cit. 205. 1839. (T.: *de la Sagra s. n.* in Herb. Paris.).
Triumfetta Lindeniana Turcz. in Bull. Soc. Nat. Moscou 31^1:229. 1858. (T.: *Linden 59*).
Triumfetta Botteriana Turcz. loc. cit. 32^1:260. 1859. (T.: *Botteri 773*).
Triumfetta Orizaba Turcz. loc. cit. 261. 1859. (T.: *Botteri 771*).
Triumfetta Josefina Polak. in Linnaea 41:552. 1877. (T.: *Polakowsky 523*).
Triumfetta vincentina Urb. Symb. Ant. 5:414. 1908. (T.: *H. H. & G. W. Smith 1057*).
Triumfetta valenciensis R. Kunth, in Fedde's Rep. Sp. Nov. Beih. 43:464. 1927. (T.: *Pittier 8677*).
Triumfetta panamensis I. M. Johnston, in Sargentia 8:194. 1949. (T.:*Johnston 1112*).

Shrubs about 1–2 m. high; branches and inflorescence axes with many long, spreading hairs. Leaves broadly ovate, usually 3-lobed, 9–10 cm. long and 7–8 cm. wide, the base rounded to subcordate, the tip acuminate, the serrations very irregular, unequal and blunt, both surfaces lightly pubescent with both stellate and simple hairs, the latter prominent, long, either spreading or appressed; petioles about 4–6 cm. long, much shorter in the bracts, very densely tomentose with long simple and stellate hairs. Inflorescences axillary, the cymes of 2 or 3 cymules, the bracts broadly elliptical, the subtending bracteoles prominent, the flowering peduncles 4–7 mm. long, the pedicels 3–4 mm. long. Flowers hermaphrodite, the buds oblongoid, 7–11 mm. long slightly before anthesis, constricted about the middle, the apical appendages slender, 2–3 mm. long, lightly pubescent; sepals oblong, 8–13 mm. long including the appendages, long-hirsute without, glabrescent within; petals broadly obovate, about 8–9 mm. long and 3–4 mm. wide, the claw about 2 mm. long, densely plumose; gonophore slender, about 1 mm. long and 0.5 mm. wide, the glands elliptical, subequalling the gonophore; urceolus short, 0.25–0.50 mm. high, not lobed, distinctly ciliate; stamens 25–30, the filaments glabrous, without serrations; ovary suborbicular, about 1.5 mm. long, the spinules numerous, recurved, the style 8–9 mm. long, the stigma acute. Fruit spheroid, the body about 3–4 mm. in diameter at maturity, 3-loculate, each cell 2-seeded, the spines slender, about 75, retrorsely pilosulose, about 3 mm. long; seeds lenticular, 2–3 mm. long and about 2 mm. wide.

A widespread weedy species of tropical America, which grows in waste lands, cut-over forest areas, and on hill-slopes, up to an altitude of about 2000 m.; flowering and fruiting from late July to early December in its northern range, from October to January in its middle, and from November to April in its southern range.

The appressed simple hairs on both surfaces of the leaves, the broadly obovate petals, and the densely pilosulose spines distinguish this species from *T. semitriloba*.

MEXICO: GUERRERO: Galeana, Carrizo to Pie de la Cuesta, *Hinton 14735* (MICH). JALISCO: Atoyac, *Kerber 135* (G). MÉXICO: Temascaltépec, Bejucos, alt. 610 m., *Hinton 2021* (K). MICHOACAN: Cordillera, alt. 3000 ped., *Galeotti 4156* (BR, P); exact locality

lacking, *Galeotti 4053* (BR, P). OAXACA: near Etla, *Pringle 5718* (MICH); exact locality lacking, alt. 1750 m., *Conzatti & Gonzalez 1054* (GH); *Liebmann 515* (US). TAMAULIPAS: Río de la Ternera, *Purpus 8277* (NY, UC, US); Tampico, *Berlandier 71* (G, FM photo). VERA CRUZ: Jalapa, *F. W. Johnson s. n.* (NY); Jalapa, *Linden s. n.* (K), *59* (G, FM photo), *771* (G, K, P, FM photo, Mo), *772* (P), *773* (K, P, FM photo); Orizaba and vicinity, *Botteri 1089* (US), *Bourgeau 2846* (BR, G, P), *Müller 1600* (BR); Zacuapan, *Galeotti 7040* (BR). YUCATAN: Izamal, *Gaumer 901, 1005* (BR, Mo), *1440* (Mo); Temax, *Gaumer 2130* (Mo); Calotmul, *Gaumer 2131* (BR); Chichankanab, *Gaumer 2035* (Mo); Xnocac, *Gaumer 23469* (Mo). DATA INCOMPLETE: *Linden 79* (BR), *211* (BR); *Hahn 65, 66* (P); *Keerl s. n.* (P).

BRITISH HONDURAS: exact locality lacking, *Peck 240* (K).

GUATEMALA: ALTA VERAPAZ: Cobán, alt. 1350 m., *Tuerckheim II 1957* (BR, Mo), alt. 4300 pp., *Tuerckheim 1359* (Mo); Samac to Chamá, alt. 2500 ft., *H. Johnson 781* (US). DATA INCOMPLETE: *Savage s. n.* (P).

NICARAGUA: SEGOVIA: environ de Granade, alt. 40 m., *Lévy 389* (G, P).

COSTA RICA: ALAJUELA: collins de San Pedro en San Ramon, alt. 1050–1075 m., *Brenes 601* (FM). CARTAGO: northwest slope of Cerro Carpintera, above La Unión, Tres Ríos, alt. 1320–1500 m., *Dodge & Thomas 4828* (Mo). GUANACASTE: defrichements sur les bords du Tiliri, *Tonduz 7208* (BR, GH). HEREDIA: Vera Blanca de Sarapiqui, between Poas and Barba volcanoes, alt. 1710 m., *Skutch 3374* (Mo). SAN JOSÉ: vicinity of El General, alt. 975 m., *Skutch 2914* (GH, Mo); heights of La Carpintera, vicinity of Tres Ríos, *Allen 524* (GH, Mo); Hacienda San Francisco de Guadeloupe, alt. 1150 m., *Pittier 8472* (BR, GH, Mo), *7160* (BR); San José, *Pittier 42* (BR); Piedra Blanca, *Tonduz 1267* (BR). DATA INCOMPLETE: *Tonduz 10925* (BR, GH, K, NY); *Endress 33* (K).

PANAMA: CANAL ZONE: vicinity of Miraflores, *P. & G. White 52* (GH, Mo); Gamboa, *Standley 28511* (GH). CHIRIQUÍ: vicinity of Bajo Mona and Quebrada Chiquero, alt. 1500 m., *Woodson & Schery 592* (Mo); Boquete, alt. 4000 ft., *Davidson 861* (Mo). PANAMÁ: Agricultural Experimental Station at Matías Hernández, *Pittier 6925* (GH, Mo); along the Corozal road, near Panamá, *Standley 26789* (GH); San José Island, about 55 miles s. se. of Balboa, *Johnston 1112* (GH). DATA INCOMPLETE: *S. Hayes 155* (GH), *325* (NY).

CUBA: LAS VILLAS: in Magdalena, Cayamas, *Baker 2490* (UC). ORIENTE: vicinity of Baracoa, *Pollard, Palmer & Palmer 32* (Mo); exact locality lacking, *Ekman 81* (S). PINAR DEL RIO: Sierra de Anafe, *Wilson & Leon 11298* (Mo). ISLE OF PINES: near Nueva Gerona, *Curtiss 234* (Mo).

VIRGIN ISLANDS: SAINT CROIX: Bassin yard, *Ricksecker 80* (Mo), *136* (Mo, NY).

SAINT VINCENT: Chateau Belair, *Beard 1390* (Mo); *H. H. & G. W. Smith 1057* (GH), *1943* (GH).

TOBAGO: Friendship, *R. O. Williams 11041* (TRIN).

TRINIDAD: Laventille Hills near Port-of-Spain, *Broadway 7617* (G, Mo); Chancellor Road, St. Ann, *Broadway 5242* (Mo), *R. O. Williams 11726, 11932* (TRIN); St. Ann, *Broadway 4415A, 4415B* (TRIN); Hort. Trin., Back Lookout, *Broadway 3681* (TRIN).

COLOMBIA: ANTIOQUÍA: Hatillo, *Bro. Daniel 412* (US); Tablaza, Caldas, *Gartner N. 8* (US); vicinity of Medellín, *Robledo & Yepes 24* (US); Medellín, alt. 1500 m., *Archer 730* (US). ATLÁNTICO: Barranquilla and vicinity, *Bro. Elias 699, 1353* (US); Piojó, Los Mameyales, alt. 350–400 m., *Dugand & Garcia B. 2408* (US); Los Pendales, camino a Santacruz, alt. 5–10 m., *Dugand & Jaramillo 2832* (US). BOGOTA: prope S. Fé de Bogota, alt. 1360 hex., *Bonpland s. n.* (P, FM photo, Mo); Gachata, alt. 1600 m., *Triana s. n.* (P). BOLIVAR: Carthagena, *Billberg 496* (S). BOYACA: region of Mt. Chapon, extreme western part of Dept. Boyaca, *Lawrance 157* (US). CALDAS: Chinchiná, alt. 1350–1400 m., *Cuatrecasas 23100* (FM). CAUCA: Popayán, alt. 1700–2000 m., *Lehmann 5522* (US), alt. 1740 m., *Lehmann 3553* (G, US); entre Popayán y Cajeti (Hacia Tambo), alt. 1700 m., *Cuatrecasas 13839* (FM). CUNDINAMARCA: La Vega, alt. 1300 m., *Arbelaez & Cuatrecasas 5344* (US); Sasaima, *Bro. José 25E* (US). MAGDALENA: vicinity of Cristobal Colon, *Broadway 294* (US). NORTE DE SANTANDER: region del Sarare, Hoya del Río Chitagá, sobre La Cubaya, alt. 1600–1800 m., *Cuatrecasas, Schultes & Smith 12143* (US); Ocaña, alt. 3500 pp., *Schlim 210* (BR). SANTANDER: northern slope of Mesa de Los Santos, alt. 1000–1500 m., *Killip & Smith 15388* (US). TOLIMA:

La Virginia Libano, alt. 1200–1500 m., *Pennell 3282* (US). VALLE: norte de Albán, alt. 2100 m., *Dugand & Jaramillo 3058* (US); La Cumbre, Cordillera Occidental, alt. 1500–1700 m., *Pennell 5213* (US); Cordillera Occidental, Vertiente Occidental, alt. 1770–2260 m., *Cuatrecasas 18544, 18623* (FM), *22172* (FM); Alto del Dinde, entre Cartago y Alcala, alt. 1200–1600 m., *Cuatrecasas 22919* (FM). DATA INCOMPLETE: *Cuatrecasas 4682, 7794* (US); *Bro. Heriberto 479* (US).

VENEZUELA: ARAGUA: Maracay, *Cornelio 64* (US), *Vogl 31* (S). CARABOBO: vicinity of Valencia, alt. 400–800 m., *Pittier 8675, 8677* (US). DISTRITO FEDERAL: Las Adjuntas, *Allart 506* (G, NY, US); lower Catuche, wood above Caracas, *Pittier 7535* (US); Caracas and vicinity, *Bailey & Bailey 286* (US). MERIDA: 3 miles west and 2 miles south of Mérida, *Reed 308* (US); Tabay, alt. 1800–1900 m., *Gehriger 447* (G, US); prope coloniam Tovar, *Fendler 123* (Mo.) MIRANDA: between Las Canales and El Encanto, *Lasser 671* (US). ZAMORA: La Union, Edo. Bolivar, *L. Williams 11226* (US).

BRAZIL: BAHIA: Carpicha, *Blanchet 799* (G); Jacobina, *Blanchet 3749* (BR, G, Mo). CEARA: exact locality lacking, *St. Hilaire Al. 156* (P); *Allemao s. n.* (R); *Rocha 6* (US). PARANÁ: vicinity of Paraná, *Dusén, 22* (S). PERNAMBUCO: Tapera, *Pickel 2727, 2727a* (US). RIO DE JANIERO: Serra do Itatiaya, Nopasto, *Sampaio 4143* (R). RIO GRANDE DO SUL: Porto Alegre, *Reineck & Czermak 329* (P). SÃO PAULO: vicinity of São Paulo, *Puiggari 3328* (P), *Vidal s. n.* (R). DATA INCOMPLETE: *Regnell I 102b* (S); Nazareth, *Jobert 1117* (P).

ECUADOR: GUAYAS: vicinity of Guayaquil, *Mille 8* (NY), *198* (US), *Rose & Rose 22453* (NY, US); vicinity of La Chonta, *Rose, Pachano & Rose 23474* (NY, US); 8 km. north of Guayaquil, *Beetle 8941, 8988* (US); Milagro, alt. 50 m., *Hitchcock 20220* (US); vicinity of Las Juntas, *Rose, Pachano & Rose 23302* (US); vicinity of Huigra, *Rose & Rose 22572* (US).

PERU: CAJAMARCA: San Miguel, Urubamba Valley, alt. 1800 m., *Cook & Gilbert 891* (US). CUZCO: Prov. Urubamba, Machupicchu, alt. 2100 m., *Vargas 795* (Mo, US).

BOLIVIA: TARIJA: Carapari, *Fries 1349* (S).

PARAGUAY: Villa Rica, dans les forets, *Balansa 2325* (G, P); Caaguazú, *Balansa 2326* (BR, G, P); Centralis, near Lake Ypacari, *Hassler 11703* (Mo, US).

ARGENTINA: JUJUY: exact locality lacking, *Fries 52* (S). MISIONES: San Ignacio, *Quiroga 7674, 7675* (S).

31. TRIUMFETTA OBSCURA St. Hil. Fl. Bras. Merid. 1:222. 1825. (T.: *St. Hilaire C282* in Herb. Paris.).

Slender shrubs 1–2 m. high; older branches terete, glabrous, the bark with many shallow, longitudinal ridges, minutely lenticellate, the younger stems and inflorescence axes scurfy, slender with few short, coarse, stellate hairs. Leaves elliptical, more than twice as long as broad, sometimes very obscurely 3-lobed, 11–13 cm. long and 4–6 cm. wide, the base cuneate to rounded, never cordate, the tip gradually and narrowly long-acuminate, the serrations double and rather regular, both surfaces very lightly pubescent with few short, stellate hairs, glabrescent; petioles 3–5 cm. long, slender, scurfy, with many short separate tufts of stellate hairs. Inflorescences axillary, rarely terminal, the cymes of 2–3 cymules, the subtending bracts of the same general shape as the vegetative leaves, the flowering peduncles about 3 mm. long, the pedicels 2–3 mm. long, the bracteoles prominent. Flowers hermaphrodite, the buds narrowly oblongoid, 6–8 mm. long slightly before anthesis, the apical appendages about 1 mm. long, lightly stellate-pubescent; sepals elliptical, 6–9 mm. long, greenish with many short separate tufts of stellate hairs without, brownish and glabrate within; petals linear to narrowly obovate, subequalling the sepals, the claw 1–2 mm. long, lightly plumose; gonophore slender,

about 0.5 mm. long, the glands spherical to slightly oblong, about half the length of the gonophore; urceolus short, about 0.25 mm. high, distinctly 5-lobed, lightly ciliate; stamens 20, the filaments retrorsely 4- to 6-serrate; ovary ovoid, about 1 mm. long, the spinules numerous, recurved, the style 5–6 mm. long, the stigma acute. Fruit orbicular, the body 3–4 mm. in diameter at maturity, very lightly pubescent, 3-loculate, each 2-seeded, the spines slender, 100 or more, about 3 mm. long, slightly retrorsely pilosulose; seeds pyriform, small, about 1.5 mm. long and wide, the funicular groove prominent.

Small trailing shrubs usually growing in forests at altitudes of 1000–1500 m., with scattered distribution; flowering and fruiting in its northern range from October to December and in its southern range from January to about the middle of April.

VENEZUELA: MIRANDA: San Antonia, near Las Mostazas, alt. 1200 m., *Allart 266* (NY, US). MONAGAS: between La Sabana de Las Piedras and Cerro Negro, northwest of Caripe, alt. 1200–1500 m., *Steyermark 61822* (FM, Mo).

BRAZIL: DISTRITO FEDERAL: trail between Sylvestre and Paineira, *L. B. Smith 2253* (US). MINAS GERAIS: Fazenda da Cachoeira, Municipio de Tambos, *Barreto 1620* (R). PARANA: Ponta Grossa, in silva, *Dusén 7551* (Mo, S). RIO DE JANEIRO: circa Sabastianopol, *St. Hilaire C2. 82* (P); Sebastianopol, *Martius 87* (BR), *88* (BR, Mo, NY, S); exact locality lacking, *Luschnath s. n.* (S); *Vauthier 431* (G); *Widgren 92* (S). RIO GRANDE DO SUL: Porto Alegre, *Reineck 220* (S). SÃO PAULO: opposite Santos, *Lindberg 692* (BR); Santos, *Mosén 3264* (S); Santa Anna, *Brade 5900* (S). DATA INCOMPLETE: *Ackermann s. n.* (BR); *Burchell 2486* (BR); *Fryer s. n.* (S); *Riedel 109* (BR, S); *Luschnath s. n.* (BR); *Raben 451* (BR).

ARGENTINA: MISIONES: Loreta, in silva, *Ekman 200* (S).

This species may be distinguished from *T. semitriloba* by its narrowly elliptic, nearly glabrate leaves and by the small apical appendages on the sepals. On a fuller knowledge, it is quite possible that *T. obscura* might be assigned a subordinate rank under *T. semitriloba*.

32. TRIUMFETTA ACRACANTHA Hochr. in Ann. Conserv. Jard. Bot. Genève 18:111. 1914. (T.: *Langlassé 505*).

Small shrubs about 1.5 m. tall; branches and inflorescence axes smooth, brownish, glabrescent. Leaves ovate-elliptic, slightly 3-lobed, about 10–11 cm. long and 4–5 cm. wide, the base rounded or obtuse, the tip gradually and narrowly acuminate, rather equally and doubly serrate, both surfaces with very few small tufts of stellate hairs, nearly glabrate; petioles slender, about 4–6 cm. long, slightly pubescent. Inflorescences usually axillary, sometimes terminal, the cymes of 2 cymules rather lax, the bracts elliptical to narrowly ovate, the flowering peduncles 2–3 mm. long, the pedicels about 2 mm. long. Flowers hermaphrodite, the buds oblongoid, 7–8 mm. long slightly before anthesis, slightly constricted towards the base, the apical appendages slender, 2–3 mm. long, glabrescent; sepals oblong, about 8–9 mm. long including the apical appendages, lightly stellate-pubescent without and glabrescent within; petals lanceolate, 3–5 mm. long, the claw about 2 mm. long, sparsely plumose; gonophore stout, about 1 mm. long and 1.5 mm. thick, the glands spherical, about 0.75 mm. long; urceolus about 0.5 mm. high,

indistinctly lobed, lightly ciliate; stamens 20, the filaments smooth, slightly pubescent towards the base; ovary ovoid, about 1 mm. long, the spinules numerous, recurved, the style slender, about 6 mm. long, the stigma briefly 3-lobed. Fruit orbicular, the body about 3 mm. thick at maturity, lightly stellate-pubescent, 3-loculate, each cell 2-seeded, the spines slender, about 75, retrorsely pilosulose.

Small shrub of western Mexico growing at low elevations, usually between altitudes of 100 and 200 m.; flowering and fruiting from September to December.

MEXICO: COLIMA: Manzanillo, *E. Palmer 902* (NY). GUERRERO: Baqueta, alt. 200 m., *Langlassé 505* (G, GH, US); Atoyac, Galeana, alt. 160 m., *Hinton 10911* (GH). SINALOA: La Noria, foothills, alt. 800 ft., *Mexia 333* (UC); Capule, alt. 200 m., *Ortega 6083* (US); Ymala, vicinity of Culican, *E. Palmer 1683* (US); vicinity of Culican, *Brandegee s. n.* (UC).

The glabrescent leaves and sepals, together with the regularity and the fineness of the serrations, clearly distinguish this species from *T. semitriloba.*

33. TRIUMFETTA ALTHAEOIDES Lam. Encyc. Meth. 3:420. 1789. (T.: "Cayenne", *Stoupy s. n.* in Herb. Paris.).

Triumfetta microphylla Vahl, Eclog. Amer. 2:34. 1796. (T.: "Br. Guyana", *von Rohr s. n.* in Herb. Copenhagen).
Triumfetta surinamensis Steud. Flora 26:755. 1843. (T.: *Hostmann 605*).
Triumfetta dichotoma Turcz. in Bull. Soc. Nat. Moscou 32^1:261. 1859. (T.: *Regel 12453*).
Triumfetta semitriloba var. *surinamensis* (Steud.) Hochr. in Ann. Conserv. Jard. Bot. Genève 18:95. 1914.
Triumfetta semitriloba f. *althaeoides* (Lam.) Uittien in Pulle, Fl. Surinam 3:56. 1932.

Bushy, spreading shrubs about 2 m. high; older branches lightly ferruginous-pubescent, the younger ones and the inflorescence axes more densely so, slightly scurfy. Leaves broadly ovate, 12–14 cm. long and 11–13 cm. wide, generally not lobed, sometimes obscurely 3-lobed, the base shallowly cordate, the tip gradually and narrowly acuminate, the serrations rather regular, generally glandular at the base, with 4 prominent glands on the petiole at the basal sinus, the upper surface lightly stellate-tomentose, the lower more densely and coarsely so; petioles 4–6 cm. long, stout, densely tomentose. Inflorescences on terminal branches, the cymes of 3–4 cymules, usually in the axils of the bracts, condensed in dense nodose clusters, the flowering peduncles 3–5 mm. long, the pedicels short, usually 1–2 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, about 6 mm. long at anthesis, the apical appendages about 1 mm. long, nearly obsolete; sepals broadly elliptical, 6–7 mm. long, densely ferruginous-tomentose without, glabrescent within; petals linear, 3–4 mm. long, the claw about 1–2 mm. long, lightly plumose; gonophore stout, about 0.75 mm. long and 1.0–1.5 mm. wide, the glands spherical, small; urceolus short, less than 0.5 mm. high, 5-lobed, lightly ciliate; stamens 20, the filaments glabrous, retrorsely 6-serrate; ovary orbicular, about 1.0 mm. long, the spinules numerous, recurved, the style about 5–6 mm. long, the stigma acute. Fruit orbicular, large, the body 6–8 mm. in diameter at maturity, lightly stellate-pubescent, 4- to 5-loculate, each cell 2-seeded, later falsely 8-loculate with one

Fig. 10. *Triumfetta althaeoides*

seed each, but not more than 6 seeds maturing per fruit, the spines numerous, about 200, slender, about 3 mm. long, retrorsely pilosulose; seeds pyriform, about 2 mm. long and 2.5 mm. wide, the funicular groove rather prominent.

Trinidad and northern South America; commonly growing on loose sandy soil in moist areas, usually at very low elevations, rarely ever being found above an altitude of 200 m.; fruiting and flowering in its northern range from August to November, and in its southern range from April to July.

TRINIDAD: Maraval, *Broadway 7065* (FM, G, Mo, S); Erin, *Broadway 7797* (Mo, S); Inois, *Broadway 8472* (Mo, TRIN); *Collins 4411* (Mo, TRIN); *Alexander 4597* (TRIN); collector not mentioned, *651, 1106* (TRIN).

COLOMBIA: ANTIOQUIA: La Serrania entre ríos Ariari y Meta, en Angostura, alt. 240 m., *Cuatrecasas 7782* (US).

BRITISH GUIANA: vicinity of Bartica, on the Essequibo River, *De la Cruz 1913* (Mo, NY, US); vicinity of Wismar, on the Demerara River, *De la Cruz 2456* (Mo, NY, US);

Waramuri Mission, Moruka River, Pomeroon Dist., *De la Cruz 1099* (US), *2563* (Mo, NY, US); Waini River, Northwest Dist., *De la Cruz 3628* (Mo, NY, UC, US); Wanama River, Northwest Dist., *De la Cruz 3951* (Mo, US); Moruka River, Pomeroon Dist., *De la Cruz 4537* (Mo, US); Penal Settlement, *Hitchcock 17088* (US). DATA INCOMPLETE: *Schomburgk 81* (P); *von Rohr s. n.* (C, FM photo).

SURINAM: prope Poclebantze, *Kegel 57* (P); *Hostmann 605* (Mo, P, U); *Focke 634* (U).

FRENCH GUIANA: Cayenne, *Sagot s. n.* (P), *Soubirou s. n.* (P), *Jelski s. n.* (S, U); vicinity of Cayenne, *Broadway 238, 286* (US). DATA INCOMPLETE: *Le Prieur 117* (P); *C. Richard s. n.* (P); *Leblond s. n.* (P).

BRAZIL: AMAZONAS: Basin of Río Solimoes, Munic. São Paulo de Olivença, near Palmeres, *Krukoff 8460* (BR, Mo, NY). BAHIA: Ilhoes, *Curran 435* (NY, US); *Salzmann 75* (G, Mo). MARANHÃO: Island of São Luiz, *Frões 11838* (US). MATO GROSSO: Cuiabá, *Malme 1538* (R, S, US); Santa Ana da Chapada, *Malme s. n.* (S). PARÁ: northeast of San Izabel, vicinity of Belem, *F. Drouet 2042* (Mo, R, US); Ilha do Mosqueiro, near Pará, *Killip & Smith 30499* (US); Belem, *Dahlgren & Sella 359, 761* (US), *A. Silva 9* (US), *Baldwin 4524* (US); locality not mentioned, *Goeldi 1097* (NY, US); *Prentiss s. n.* (NY). PERNAMBUCO: Tapera, Recife, *Pickel 3446* (US). RIO DE JANEIRO: Raiz da Serra de Petropolis, *Gomes 68* (R). SÃO PAULO: locality not mentioned, *Burchell 4484, 7218* (BR).

PERU: LORETO: Ost-Peru, Stromgebiet des Maranon von Iquitos, *Tessmann 3592* (S); Balsapuerto, alt. 220 m., *Klug 3054* (Mo, US); Mishuyacu, near Iquitos, alt. 100 m., *Klug 1086, 1289* (US), *Killip & Smith 27240* (US); Punchana, near Iquitos, *L. Williams 1316, 1324* (US); Caballo-Cocha on the Amazon, *L. Williams 2063* (US).

BOLIVIA: COCHABAMBA: exact locality lacking, *D'Orbigny 596* (P). LA PAZ: Mapiri, *R. S. Williams 787* (US).

Despite the fact that this species has often been treated as synonymous with *T. semitriloba*, it is definitely not conspecific with it. Its large orbicular 8-loculate fruit with numerous long slender spines, and its broadly ovate, undivided leaves with 4 conspicuous glands on the petiole at the basal sinus are two of the more important characters which aid in distinguishing this weedy species from *T. semitriloba*.

34. TRIUMFETTA SEMITRILOBA Jacq. Select. Stirp. Amer. Hist. 147. 1763. (T.: *Banks Herb. s. n.* in Herb. Riksmuseet, Stockholm).

Triumfetta triloba Lam. Ency. Meth. 3:420. 1789. (T.: *Commerson s. n.* in Herb. Paris.).
Triumfetta hirta Vahl, Symb. Bot. Pl. 3:63. 1794. (T.: "St. Martha", *Ryan s. n.* in Herb. Copenhagen).
Triumfetta rubricaulis HBK. Nov. Gen. & Sp. 5:342. 1821. (T.: "Caracas", *Bonpland s. n.* in Herb. Paris.).
Triumfetta havanensis HBK. loc. cit. 345. 1821. (T.: "Insula Cuba, prope Havanam", *Bonpland s. n.* in Herb. Paris.).
Triumfetta ovata DC. Prod. 1:507. 1824. (T.: "Antilles", collector unknown in Herb. Deless.).
Triumfetta oxyphylla DC. loc. cit. 508. 1824. (T.: "Novae-Hispaniae", *Sessé & Mociño s. n.* in Herb. Deless.).
Triumfetta tricuspis St. Hil. Fl. Bras. Merid. 1:224. 1825. (T.: "Villa-Rica", *St. Hilaire s. n.* in Herb. Paris.).
Triumfetta acutiloba DC. Pl. Rar. Jard. Genève, 64. 1829. (T.: "Havanne", *S. Burat s. n.* in Herb. Deless.).
Triumfetta Thonningiana DC. loc. cit. 1829. (T.: *Thonning s. n.* in Herb. Deless.).
Triumfetta tiliaefolia Vahl ex DC. loc. cit. 1829. (T.: *West s. n.* in Herb. Deless.).

Fig. 11. *Triumfetta semitriloba*

Triumfetta semitriloba var. *brasiliensis* K. Schum. in Mart. Fl. Bras. 12^3:135. 1886. (T.: *Blanchet 799*).
Triumfetta semitriloba var. *Martiana* K. Schum. loc. cit. 135. 1886, in part. (T.: *Martius 1263*).
Triumfetta semitriloba var. *typica* K. Schum. loc. cit. 1886.
Triumfetta semitriloba havanensis (HBK.) Millsp. in Field Mus. Publ. Bot. 1:507. 1902.
Triumfetta semitriloba var. *Berlandieri* Hochr. in Ann. Conserv. Jard. Bot. Genève 18:95. 1914. (T.: *Berlandier 71*).
Triumfetta Sloanei Fawc. & Rend. in Jour. Bot. 59: 225. 1921. (T.: *Ridley s. n.* in Herb. Kew.).
Heliocarpus hirtus (Vahl) Will. & Sandw. in Fl. Trin. & Tobago 1:111. 1929.

Shrubs 1–2 m. high; older branches terete, glabrescent, the bark reddish, prominently lenticellate, the younger ones and inflorescence axes rough, slender, scurfy,

with short, coarse, stellate tomentum. Leaves generally broadly ovate to 3-lobate, the shape and size extremely variable even on the same plant, usually about 6–8 cm. long and 4–6 cm. wide, the base either cuneate or rounded, very rarely subcordate, the terminal lobe long-acuminate, the laterals usually blunt, but sometimes all 3 lobes narrowly and gradually acuminate, the serrations extremely irregular, usually glandular, both surfaces rather densely and coarsely stellate-pubescent; petioles 3–6 cm. long, slender, scurfy with short, separate tufts of stellate hairs. Inflorescences axillary, rarely terminal, the cymes of 2–3 cymules in the axils of the bracts, the bracts narrowly elliptical, very rarely obscurely 3-lobed, the flowering peduncles 2–3 mm. long, the pedicels about 3 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, about 5–8 mm. long slightly before anthesis, the apical appendages 1–2 mm. long, lightly stellate-pubescent; sepals elliptical, 6–10 mm. long including the apical appendages, greenish and rather lightly stellate-pubescent without, yellow-brown and glabrescent within; petals elliptical to narrowly obovate, subequalling the sepals, the claw 2–3 mm. long, rather densely plumose; gonophore about 0.75 mm. long, rather slender, the glands oblong, about half as long as or subequalling the gonophore; urceolus rather short, 0.25–0.50 mm. high, densely ciliate; stamens 15–25, the filaments glabrous, retrorsely 4-serrate; ovary ovoid, about 1 mm. long, the spinules numerous, recurved, the style 6–8 mm. long, the stigma usually acute, very rarely 3-parted. Fruit orbicular, the body 3–5 mm. in diameter at maturity, lightly to rather densely stellate-pubescent, 3-loculate, each cell 2-seeded, though very rarely all the 6 seeds maturing, the spines 50–75, 2–3 mm. long, slender, retrorsely pilosulose at the base from half to three-quarters of its length; seeds pyriform, about 2 mm. long and wide, the funicular groove prominent.

A common weed of the tropics, which finds its habitat usually in abandoned fields or cut-over forest areas, and in general being a nuisance to both man and his animals, growing from sea-level to about an elevation of 2000 m. It is found principally in the warmer regions of the New World, and less abundantly in tropical Africa. Flowers and fruits in its northern range from October to March, in its central range from December to May, and in its southern range from March to July.

This species may be recognized by its leaves which generally tend to be bluntly 3-lobed, bearing only short, scabrous, stellate hairs on both surfaces, together with either its elongoid flowers, which are 6–10 mm. long with linear-elliptic petals, or its fruits with 3, 2-seeded locules, and about 50–75 retrorsely pilosulose spines.

MEXICO: CAMPECHE: Tuxpeña, *Lundell 953* (Mo). CHIHUAHUA: west of Chuchuichupa, *LeSueur 957* (Mo); Guasaremos, Río Mayo, tropical upper Sonoran margin, *Gentry 1884* (Mo); Hacienda San Miguel, near Batolopes, *E. Palmer 23* (GH, K, US). GUERRERO: Acapulco and vicinity, *E. Palmer 605* (K, Mo, NY, UC). JALISCO: shaded slopes of the barranca near Guadalajara, *Pringle 1756* (BR, K, Mo, MICH); exact locality lacking, *Galeotti 4150* (BR). MORELOS: hills near Yantepec, alt. 4000 ft., *Pringle 9695* (K, Mo). NAYARIT: vicinity of Acaponeta, Tepic, *Rose, Standley & Russell 14212, 14279* (NY); Santiago, Tepic, *Lamb 549* (Mo); Rincon de Mateo, near Yxtlan, alt. 1100 m., *Mexia 775* (Mo); Tepic, *M. E. Jones s. n.* (UC). SAN LUIS POTOSI: en route from San Luis Potosi to Tampico, *E.*

Palmer 1069 (K, Mo); Tamasunchale, *Kenoyer s. n.* (Mo). SINALOA: Las Mesas, Sierra Suratato, alt. 3000 ft., *Gentry 6623* (Mo). SONORA: Sierra de Alamos, rocky canyon slope, alt. 3000 ft., *Gentry 4867* (Mo); Alamos, *E. Palmer 642* (US). TAMAULIPAS: vicinity of Tampico, *E. Palmer 72* (GH); vicinity of Gómez Farias, alt. 350 m., *E. Palmer 270* (Mo); 10 km. northwest of El Progresso, vicinity of Ocampo, alt. 1450 m., *Stanford, Retherford & Northcraft 1048* (Mo). VERA CRUZ: Cordillera, *Galeotti 7040* (P); exact locality lacking, *Müller 204* (NY), *Gounin s. n.* (P). YUCATAN: exact locality lacking, *Gaumer 24450* (Mo).

GUATEMALA: ALTA VERAPAZ: Cubilquitz, alt. 350 m., *Tuerckheim II 227* (BR, S); Cobán, alt. 4000 ft., *H. Johnson 38* (US). PETEN: La Libertas and vicinity, *Aguilar 188* (Mo).

EL SALVADOR: SAN SALVADOR: vicinity of San Salvador, alt. 650–850 m., *Standley 22685* (NY).

COSTA RICA: data incomplete, *Solis R. 6* (Mo).

BERMUDA: Walsingham, *Harshberger s. n.* (Mo), *Flynn 76* (Mo).

BAHAMA ISLANDS: New Providence: Nassau, *Hitchcock s. n.* (Mo); *Curtiss 11* (Mo).

CUBA: HAVANA: prope Havana, *Bonpland s. n.* (P, Mo photo); Santiago de las Vegas, *Hermann 307* (Mo); La Havanne, *de la Otta s. n.* (Mo photo). LAS VILLAS: Santa Clara, Cieneguita, Dist. Cienfuegos, *Combs 115* (Mo). ORIENTE: *Wright 43* (BR, G, Mo, S); Bayate secus vias, *Ekman 2985* (S), *3413* (S); Sierra de Nipe, El Taller ad Río Piloto, *Ekman 3337* (S).

GRAND CAYMAN: *Hitchcock s. n.* (Mo).

JAMAICA: Port Morant, *Hitchcock s. n.* (Mo); Lucca, *Hitchcock s. n.* (Mo); Farm Hill, *Orcutt 3436* (Mo); mountains near Kingston, *Hansen s. n.* (Mo); *Cumming s. n.* (G); Porto Antonio, *Hitchcock s. n.* (Mo); Lloyd, *Hitchcock 1014* (Mo); Constant Spring, *Ridley s. n.* (K).

HAITI: La Tortue, between Palmiste and Embrouchure de la Thochelle, *Ekman 4184* (S); La Tortue, main ridges at Binquette, *Ekman 4229* (S); Roseaux, valley of Roseaux River, *Seibert 1774* (Mo); prope Sarrasin, *Buch 586* (S).

DOMINICAN REPUBLIC: Dist. Moncion, Prov. Monty Cristy, alt. 375 m., *Valeur 411* (Mo); "Sylvania", alt. 1500–1800 ft., *Cooper III 25* (Mo, NY); St. Domingo City, at Guibia, *Ekman 10945* (S); St. Cristobal, *Tuerckheim 2623* (BR, Mo, S).

PUERTO RICO: Ciales, Bayamon, *Otero 363* (Mo); Rincon, ad Tuntas, *Sintenis 5652* (Mo); near Mayaguez, *Thevshohn 30* (Mo), *Blauner 171* (G), *Heller 4444* (Mo).

VIRGIN ISLANDS: SAINT THOMAS. Signal Hill, alt. 1200 ft., *Eggers s. n.* (Mo). SAINT CROIX: Bassin, *Ricksecker 138* (Mo), *225* (FM); *Thompson 1018* (S).

FRENCH WEST INDIES: SAINT BARTHELEMY: *von Goes s. n.* (S); *Forström s. n.* (S). GUADELOUPE: Pointe-à-Pitre, *Hammarlund 29* (S); Cascade Vaugelé, *Picard s. n.* (P); *Beaupertuis s. n.* (P). MARTINIQUE: *Belanger 560, 647* (P); Fort Royal, *Plée s. n.* (P).

SAINT VINCENT: near Kingstown, *Eggers 6940* (S).

BARBADOS: *Wright s. n.* (BR).

TOBAGO: Highmoor, *Broadway 3407* (Mo).

TRINIDAD: *Kuntze 661* (US).

COLOMBIA: MAGDALENA: exact locality lacking, *Bertero s. n.* (Mo).

VENEZUELA: DISTRITO FEDERAL: Los Venados, near Caracas, *Allart 93* (G,NY,US); near Caracas, alt. 450 m., *Bonpland s. n.* (FM photo, Mo). MERIDA: 3 miles west, 2 miles south of Mérida, *Reed 306* (US); near Galipan, on the bank near water, *Pittier 213* (G). MIRANDA: vicinity of Petare, along hills, *Pittier 9894* (G); Hacienda Paloma, alt. 900 m., *Pittier 13052* (GH, Mo, NY, US); in valley on road from El Valle to Cua, along the river, *Pittier 11974* (Mo).

BRAZIL: BAHIA: exact locality lacking, *Blanchet 3117* (G); *Luschnath 163* (BR). DISTRITO FEDERAL: Trapicheiro, *Lutz s. n.* (R). MINAS GERAIS: Campo Tiririca, alt. 590 m., *Mexia 5663* (Mo, R, US); Lagoa Santa, *Da Costa s. n.* (R); Serre Negra, *St. Hilaire 98* (P); Viçosa, Chacha Valley, *Mexia 4733* (Mo, US); exact locality lacking, *Claussen s. n.* (NY), *Martens s. n.* (BR). PARANA: Morretes, Estrada da Graciosa, Grota Funda, *Hatschbach 908* (US). RIO DE JANEIRO: Nova Friburgo, Estrada de Conego,

Velloso s. n. (R); Corcovado, *Saldanha 224, 649* (R); Petropolis, *Sampaio 7692* (R); Campos, *Sampaio 8300* (R); Ipanema, *Diogo 52* (R); Teresopolis, *Emygdio s. n.* (R); Matas do Rio Trapicheiro, *Freire & Peckolt 612, 613* (R). SÃO PAULO: Horto Florestal de Loreto, *Sampaio 4306* (R); Jaraguá, *Brade 5897* (S). DATA INCOMPLETE: *Regnell II 286* (S); *Urteri 12* (G).

ECUADOR: GUAYAS: 21 km. southwest of Guayaquil, alt. 40 m., *Worth, Morrison & Horton 8941* (Mo); Sudl. Naranjapata, alt. 550 m., *Schimpff 587* (Mo, US).

PERU: LIMA: exact locality lacking, *Anderson s. n.* (S). LORETO: lower Río Huallaga, *L. Williams 4360* (US). SAN MARTIN: San Roque, alt. 1350–1500 m., *L. Williams 7160* (US).

BOLIVIA: BENI: Río Chaparé-Mamoré, alt. 250 m., *Werdermann 2166* (Mo); vicinity of Reyes, alt. 1000 ft., *Cardenas 1377* (NY). COCHABAMBA: Prov. Chapare, Wegerand, Socotol, alt. 1500 m., *Steinbach 9089* (S). LA PAZ: Yungas, *Bang 465* (FM, Mo); Mapiri, alt. 2500–5000 ft., *Rusby 1236a* (NY); Prov. Larecaja, near Sorata, alt. 2550 m., *Mandon 826* (BR, NY, S), *827* (G, S); Apolo, *R. S. Williams 193* (NY, US); Polo-Polo bei Coroico, alt. 1100 m., *Buchtien 3840* (S). SANTA CRUZ: Prov. Sara, Buena Vista, Barbechos, Río Surutú, alt. 400 m., *Steinbach 5545* (G, Mo, S); Buena Vista, Orillabasque, alt. 450 m., *Steinbach 7118, 7416* (Mo, S). DATA INCOMPLETE: *Fries 1506, 1506a* (S).

PARAGUAY: Villarica, *Jörgensen 3858* (Mo, S, US); exact locality lacking, *Morong 132* (NY).

ARGENTINA: JUJUY: en las Cercanias, *Lorentz & Hieronymus 1009* (S); Humahuaca, alt. 2800 m., *Venturi 8369* (S, US); Humahuaca, alt. 3020 m., *Claren 11715* (S). MISIONES: Santa Ana, *Rodriguez 231* (Mo).

35. TRIUMFETTA OLIGACANTHA Hochr. in Ann. Conserv. Jard. Bot. Genève 18:106. 1914. (T.: *Pavon s. n.* in Herb. Deless.).

Small shrubs; branches and inflorescence axes smooth, scurfy, ferruginous-tomentose. Leaves broadly ovate, about 9–10 cm. long and 6–8 cm. wide, the base obtuse, the tip gradually long-acuminate, the serrations rather regular, the basal ones generally glandular, the upper surface lightly stellate-pubescent, the lower more densely so; petioles about 3–6 cm. long, densely pubescent. Inflorescences axillary, the cymes of 3–4 cymules, rather lax, the flowering peduncles about 8–10 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 6–8 mm. long slightly before anthesis, slightly constricted in the middle, the apical appendages large, about 3 mm. long, slightly pubescent; sepals oblong, 8–11 mm. long including the apical appendages, densely tomentose without, glabrescent within; petals narrowly obovate, 6–7 mm. long, the claw 2–3 mm. long, shortly plumose; gonophore slender, about 0.75 mm. long, the glands narrowly elliptical; urceolus small, about 0.5 mm. high, indistinctly lobed, slightly ciliate; stamens about 30, the filaments smooth, glabrous; ovary small, orbicular, about 1 mm. long, the spinules about 35, recurved, the style about 8–9 mm. long, the stigma acute. Fruit orbicular, the body about 2–3 mm. in diameter at maturity, matted cinereous-tomentose, 3-loculate, each cell 1-seeded, the spines 25–40, 2–3 mm. long, retrorsely pilosulose; mature seed pyriform, about 1.5 mm. long and wide, the funicular groove prominent.

Known only from a few collections, mostly from Ecuador, and one (the type) probably from Peru. Apparently rare plants, which are usually found at low elevations. Flowering and fruiting from June to October.

Ecuador: guayas: Duran, Westabhang, alt. 40 m., *Schimpff 1078* (Mo); Guayaquil, alt. 50 m., *Hitchcock 20153* (US). data incomplete: Terecita, *Stevens 161* (US); *Fraser s. n.* (G).

Peru (?): *Pavon s. n.* (G).

Though rather poorly represented in the herbaria, this is one of the more distinct species in the "*semitriloba* complex." It is easily identified by its undivided, caudate-acuminate leaves, by its relatively long apical appendages of the sepals, and also by its fruits, which have only a few (25–40) spines.

36. Triumfetta Lappula L. Sp. Pl. ed. 1. 444. 1753.

Triumfetta heterophylla Lam. Encyc. Meth. 3:420. 1789. (T.: "St. Domingo", *Poiteau s. n.* in Herb. Paris.).
Triumfetta sinuosa Miq. in Linnaea 22:466. 1849. (T.: *Kappler 1589*).
Triumfetta Hostmanni Miq. loc. cit. 1849. (T.: *Hostmann 499*).
Triumfetta Berteri Turcz. in Bull. Soc. Nat. Moscou 31^1:227. 1858. (T.: *Bertero s. n.* in Herb. Paris.).
Triumfetta Salzmanni Turcz. loc. cit. 229. 1858. (T.: *Salzmann s. n.* in Herb. Paris.).
Triumfetta quinqueloba Turcz. loc. cit. 36^1:574. 1863. (T.: *Mathews 1625*).

Fig. 12. *Triumfetta Lappula*

Tall weedy shrubs about 1–2 m. high; branches and inflorescence axes with coarse, scurfy, ferruginous tomentum. Leaves broadly ovate, usually pandurate, 3- to 5-lobed, about 8–10 cm. long and 7–9 cm. wide, the base obtuse to rounded, the tips acuminate, the serrations usually glandular, unequal and blunt, the upper surface lightly pubescent, the lower lightly tomentose to more densely so; petioles usually 6–8 cm. long, sometimes slightly longer, usually thick, very densely and coarsely pubescent. Inflorescences axillary, the cymes of 2, rarely 3, cymules, generally condensed, the bracts elliptical, very rarely obscurely 3-lobed, the flowering peduncles about 2–3 mm. long, the pedicels short, 1–2 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 3–5 mm. long slightly before anthesis, slightly constricted in the middle, the apical appendages very short, rarely absent; sepals oblong, about 4–6 mm. long, densely stellate-tomentose without, glabrescent and yellowish within; petals absent; gonophore obsolete, the glands absent; urceolus very small, nearly obsolete, not ciliate; stamens usually 10, rarely 15 or 5, the filaments glabrous, smooth; ovary ovoid, about 1.0–1.5 mm. long, the spinules numerous, recurved, the style about 3 times the length of the ovary, the stigma acute, sometimes very briefly 2-fid. Fruit orbicular, the body about 3 mm. in diameter at maturity, lightly stellate-pubescent, 3-, sometimes 2-, loculate by abortion, the spines about 50, slender, 2–3 mm. long, retrorsely pilosulose; seeds pyriform, about 1.5–2.0 mm. long and 1.0–1.5 mm. wide.

A widespread species found abundantly in the tropical Americas and less so in the eastern hemisphere. Usually growing in open places and a nuisance in cultivated paddocks, it finds its habitat from sea-level to an altitude of about 2000 m Flowers and fruits from late November to early March.

The absence of petals, gonophore, and urceolus in flower, and the retrorsely pilosulose spines, the small body and the absence of glandular gonophore in fruit, are some of the more constant characters which facilitate the identification of this species.

MEXICO: CAMPECHE: Tuxpeña, *Lundell 1188* (Mo). CHIAPAS: Escuintla, *Matuda 97* (Mo). YUCATAN: exact locality lacking, *E. P. Johnson 58* (NY).

BRITISH HONDURAS: Mullins River road, alt. 100 ft., *Schipp 868* (Mo).

HONDURAS: MORAZÁN: Francisco, along Yeguare River, alt. 900 m., *Williams & Molina 12202* (Mo). ATLANTIDA: above San Juan, west of Tela, *Yuncker 4810* (Mo).

EL SALVADOR: SAN SALVADOR: vicinity of San Salvador, alt. 650–850 m., *Standley 19091* (Mo).

NICARAGUA: CHINANDEGA: near Chinandega, *Baker 2247* (K, Mo); Volcán El Viejo, *Baker 17* (Mo). GRANADA: envr. de Granada, alt. 410 m., *Lévy 399* (G, P).

COSTA RICA: GUANACASTE: buissons autour de Nicoya, *Tonduz 13491* (G, NY, P, US). SAN JOSÉ: taillis du Rodeo de Pacaca, alt. 900 m., *Pittier 3258* (BR); au Rodeo, alt. 700–1000 m., *Pittier 1630* (BR); vicinity of El General, alt. 880 m., *Skutch 3028* (Mo). DATA INCOMPLETE: près San Mateo, alt. 200 m., *Biolley 7059* (BR); brussailles du Río Ceibo, alt. 200 m., *Pittier 6693* (BR).

PANAMA: BOCAS DEL TORO: vicinity of Chiriquí Lagoons, Old Bank Island, *Wedel 1883, 1949, 2005* (Mo); Water Valley, *Wedel 1710, 1779, 1825, 1847, 1854* (Mo); Darkland, *Wedel 2618* (Mo); Boca, littoral Atlantique, *Tonduz 9153* (BR). CANAL ZONE: Barro Colorado Island, *Shattuck 728* (Mo); vicinity of Miraflores Lake, *P. White 279* (Mo); Ancón Hill, alt. 600 ft., *R. S. Williams 21* (NY); vicinity of San Carlos, alt.

10 m., *Allen 1138* (Mo); Chagres, Isthmus of Panama, *Fendler 172* (Mo); hills between Capira and Potrero, alt. 80–130 m., *Dodge & Hunter 8626* (Mo). DATA INCOMPLETE: *S. Hayes 321, 370, 991, s. n.* (NY); *Mell s. n.* (NY).

CUBA: SANTA CLARA: Colonia Limones, Ingenio Soledad, near Cienfuegos, *Pringle 93* (Mo). ORIENTE: Santiago de las Vegas, *Baker 84* (Mo, NY, P, U); Cooper's Ranch, base of El Yunque, Mt. Baracoa, *Underwood & Earle 578* (NY). DATA INCOMPLETE: *Serre s. n.* (BR).

ANTIGUA: *Wullen s. n.* (BR).

GRAND CAYMAN: *Hitchcock s. n.* (Mo).

JAMAICA: Gray's Inn, *Orcutt 4664* (Mo); above Kingston, *Lehmann 1292* (NY); Port Morant, *Hitchcock s. n.* (Mo); Constant Springs, *Hitchcock s. n.* (Mo).

DOMINICAN REPUBLIC: Sonador, Bonao, La Vega, alt. 180 m., *Valeur 381* (Mo, NY); prope Barahona, *Fuertes 179* (Mo).

PUERTO RICO: on the Adjuntas road, 7 miles from Ponce, *Heller 6184* (Mo); Bayamon District, Santurce, *Otero 462* (Mo); Signal Hill, alt. 1100 m., *Eggers s. n.* (Mo).

VIRGIN ISLANDS: SAINT THOMAS: *Eggers 58* (S); *Krebs s. n.* (U). SAINT CROIX: Bassin yard, *Ricksecker 135* (Mo); *Benzon s. n.* (Mo).

MARTINIQUE: *Duss 1363* (Mo); *Belanger 31* (P); *Hahn 224* (P).

TOBAGO: Rocky Vale, *Broadway 3383* (Mo, S); near the Yaws Hospital, Scarborough, *Broadway s. n.* (Mo); top of Lambeau, near King's Bay, *Freeman 10254* (Mo, TRIN).

TRINIDAD: road to Blue Bassin, *McLean 7725* (Mo, TRIN); Carenage, *Fitzsimmons 3847* (TRIN); *Collins 4433* (TRIN); Chancellor's Road, *Broadway 10253* (TRIN); Diego Martin, *Reece s. n.* (TRIN); near Williamsville, *Broadway 9362* (G, U); Moruga, *Britton & Broadway 2454* (US); *Salzmann 250* (Mo).

COLOMBIA: ATLÁNTICO: Los Pendales, Hacienda Ríodulce, alt. 20–50 m., *Dugand & Jaramillo 4139* (US); Los Pendales, cerca de la laguna de Sábalo, alt. 10–30 m., *Dugand & Jaramillo 2704* (US). CAUCA: Popayán, *Garcia B. 4493* (US). LOS LLANOS: Int. El Meta, Villavicencio, alt. 500 m., *Cuatrecasas 4528, 4683* (US). MAGDALENA: Poponte, Magdalena Valley, *Allen 792* (Mo); Curinquita, *H. H. Smith 1908a* (NY). NORTE DE SANTANDER: region del Sarare, El Blanco, confluncia de los ríos Cubugón y Cobaria, alt. 320 m., *Cuatrecasas 13153* (US). SANTA MARTA: exact locality lacking, *H. H. Smith 1690* (BR, Mo, US). TOLIMA: Falán, region de Calamonte, alt. 1120 m., *Garcia B. 8380* (US). VALLE: plano del Valle del Cauca, entre Cabuyal y La Solorza, alt. 1000 m., *Cuatrecasas 14439* (FM, US); Río Canaveralejo, alt. 100 m., *Dryander 2232* (US).

VENEZUELA: DISTRITO FEDERAL: Cordillera del Avila, dry south-facing slopes above Caracas, alt. 1065–1520 m., *Steyermark 55179* (FM, Mo); Puerto La Cruz, alt. 10 m., *Pittier 11640* (G, US); La Guaira, *Boldingh s. n.* (U). MÉRIDA: prope coloniam Tovar, *Fendler 1918* (K). MIRANDA: La Malva near Las Mostazas, *Allart 278* (G, NY, US). SUCRE: Paria Peninsula, Cariaquita, *Bond, Gillin & Brown 5* (US). TRUJILLO: La Concepcion, alt. 2500 ft., *Reed 1041* (US); vicinity of Cristobal Colon, Aricagua, *Broadway 174, 405* (US). DATA INCOMPLETE: *Mathews 1625* (K).

BRAZIL: MARANHÃO: Island of São Luiz, *Froes 11839, 11852* (US). PARÃ: Boa Vista, *Carr s. n.* (US); exact locality lacking, *Sieber s. n.* (BR). DATA INCOMPLETE: *Martius A. 1264* (Mo).

ECUADOR: GUAYAS: Milagro, alt. 50 m., *Hitchcock 20221, 20239* (US). JUNIN: La Merced, alt. 700 m., *Killip & Smith 23419* (US).

PERU: LORETO: Balsapuerto, alt. 200 m., *Klug 3093* (Mo, US). SAN MARTIN: Chazuta, Río Huallaga, alt. 260 m., *Klug 4150* (Mo, US); Iquitos, alt. 100 m., *Killip & Smith 27234* (US).

BOLIVIA: COCHABAMBA: vicinity of Guanai, *Bang 1597* (Mo, S, US). LA PAZ: Charopampa, Mapiri, *Buchtien 1825* (US).

37. TRIUMFETTA **sericata** Ko Ko Lay, sp. nov.

Frutex circiter 1.5–2.0 m. altus. Ramuli graciles dense pubescentes pilis ferrugineis et stellatis et simplicibus. Folia late ovata vel profunde 3-lobata 9–12 cm. longa 7–10 cm. lata base rotundata vel subcordata apice longe acuminata

margine irregulariter serrata interdum glandulosa utrinque scabratis pilis dense canescenti-tomentosis; petiolis 7–10 cm. longis dense tomentosis. Inflorescentiae terminales, cymis cymulis 5–6, bracteis ovatis vel obscure 3-lobatis, pedunculis 2–3 mm. longis, pedicellis 2–4 mm. longis. Flores hermaphroditi, alabastro maturo oblongoideo 6–8 mm. longo; sepalis ellipticis circiter 8 mm. longis extra longe et dense stellato-tomentosis, appendiculis circiter 2 mm. longis dense plumosis; petalis ellipticis 6–7 mm. longis, unguilo circiter 2 mm. longo extra breviter plumoso; gonophoro 0.25–0.5 mm. longo, glandulis quadrangularibus circiter 0.1 mm. latis; urceolo 0.25 mm. alto non-lobato breviter ciliato; staminibus 15, filamentis usque ad 5–6 mm. longis glabris; ovario ovoideo 0.5–1.0 mm. longo, spinulis 40–50 recurvatis, stylo glabro 6–7 mm. longo, stigmate acute vel breviter 3-fido. Fructus globosus non dehiscens, corpore ipso 2–3 mm. diametro breviter stellato-pubescens mox glabrescens, 3-locularis, loculis 1-spermis, aculeis circiter 50, 2.0–2.5 mm. longis irregulariter plumosis; seminibus ovoideo-acutis circiter 0.75 mm. longis et latis.

Northwestern South America growing in open places at altitudes of 1000 to 1300 m.; flowering and fruiting from August to early December.

COLOMBIA: CAUCA: La Manuelita, near Palmira, eastern side of Cauca Valley, alt. 1100–1300 m., *Pittier 794* (NY, US); El Bordo, *Garcia B. 4472* (US). CUNDINAMARCA: El Colegio, *Joseph s. n.* (US). TOLIMA: Honda, *Joseph s. n.* (US). VALLE: Municipio de Candelaria, sur de Palmira, alt. 1200 m., *Nuñez, Araque & Barkley 18. VC. 025* (holotype in Herb. Mo. Bot. Gard. and isotype in U. S. Nat. Herb.).
ECUADOR: exact locality lacking, *Jameson s. n.* (US).

The densely tomentose leaves, the small oblongoid floral buds in dense nodose clusters, the 15 stamens and the small, dark, very lightly pubescent fruits distinguish this species. Though it has a striking superficial resemblance to *T. abutiloides*, it is not closely related to it. Its relationship with any known South American species is rather doubtful. However, it is closest to *T. brachistacantha*, known only from Oaxaca, Mexico.

38. TRIUMFETTA BRACHISTACANTHA Standl. in Field Mus. Publ. Bot. 11:167. 1936. (T.: *Bossé 8019*).

Older branches glabrate, longitudinally ridged, with many prominent white lenticels, the younger stems and inflorescence axes terete, lightly stellate-pubescent. Leaves broadly ovate, small, 1.5–2.0 cm. long and about 1.0 cm. wide, obtuse to subcordate at the base, gradually and narrowly acuminate, rather regularly and doubly serrate, the upper surface lightly stellate-pubescent, the lower more densely so; petioles short, usually not longer than 1 cm., lightly stellate-pubescent. Inflorescences axillary, the cymes of 1 or 2 cymules, rather lax, the flowering peduncles about 3 mm. long, the pedicels 3–4 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 5–7 mm. long slightly before anthesis, the apical appendages short, about 1 mm. long or less; sepals lanceolate, 7–8 mm. long including the apical appendages, lightly stellate-pubescent without; petals broadly obovate, 5–6

mm. long and 2–3 mm. wide, the claw 2–3 mm. long, densely plumose; gonophore very short, less than 0.5 mm. long, the glands oblong, small; urceolus rather short, about 0.25 mm. high, distinctly 5-lobed, briefly ciliate; stamens 15, the filaments glabrous, smooth; ovary orbicular, about 1 mm. long, the spinules numerous, recurved, the style 4–5 mm. long, the stigma acute. Fruits orbicular, small, loosely borne in small nodose clusters, the body 2–3 mm. in diameter at maturity, lightly stellate-pubescent, 3-loculate, each cell 1-seeded, the spines about 75–100, about 1 mm. long, glabrous; seeds ovoid, 1.5–2.0 mm. long and 1.0–1.5 mm. wide.

Known only from the type.

MEXICO: OAXACA: Chivela, *Bossé 8019* (FM).

39. TRIUMFETTA BARTRAMIA L. Syst. ed. 10. 1044. 1759. (Based on *Bartramia indica*).[35]

Bartramia indica L. Sp. Pl. ed. 1. 389. 1753. (T.: specimen from Hermann's Herb. now in Herb. Mus. Brit.).
Triumfetta rhomboidea Jacq. Select. Stirp. Amer. Hist. 147. 1763.
Triumfetta rhombeaefolia Sw. Prod. Veg. Ind. Occ. 76. 1788. (T.: *Swartz s. n.* in Herb, Riksmuseet, Stockholm).
Triumfetta angulata Lam. Encyc. Meth. 3:421. 1789.
Triumfetta eriocarpa St. Hil. Fl. Bras. Merid. 1:224. 1825. (T.: *Gaudichaud s. n.* in Herb. Paris.).
Triumfetta Lappula Vell. Fl. Flum. 5:*t. 5*. 1827, non L.
Triumfetta Martiana Turcz. in Bull. Soc. Nat. Moscou 31^1:228. 1858. (T.: *Martius 1263*).
Triumfetta semitriloba var. *Martiana* K. Schum. in Mart. Fl. Bras. 12^3:135. 1886, in part. (T.: *Martius 1263*).
Triumfetta rhomboidea var. *Spruceana* K. Schum. loc. cit. 133. 1886. (T.: *Blanchet 188*).
Triumfetta excisa Urb. Symb. Ant. 5:413. 1908. (T.: *Sintenis 17c*).
Triumfetta rhomboidea var. *recifensis* Monteiro, in Lilloa 3:247. 1938. (T.: *Monteiro 218b*).

Tall perennial shrubs 1–3 m. high; older branches reddish-brown, glabrous, rough, longitudinally ridged, punctate with prominent white lenticels, the younger ones and inflorescence axes terete or with very shallow longitudinal ridges, scurfy, clothed with short dense rough stellate tomentum. Leaves typically broadly ovate to rhombic-ovate, obscurely or distinctly 3-lobed, often rather deeply dissected into 3 to 5 lobes, usually 4–5 cm. long and nearly as broad, sometimes 7–8 cm. long and 6–7 cm. wide, obtuse or rounded at the base, abruptly acuminate, the serrations irregular, blunt, rarely glandular near the basal sinus, both surfaces nearly glabrate with few scattered, short, coarse, stellate hairs; petioles slender, 3–5 cm. long, briefly stellate-tomentose, scurfy. Inflorescences axillary, the cymes of 3–5 cymules, condensed in dense nodose clusters, the bracts narrowly ovate, petioles usually about 1 cm. long, the flowering peduncles 1–2 mm. long, the pedicels about 1 mm. long. Flowers hermaphrodite, the younger buds obovoid with very deeply cucullate sepals, the older ones oblongoid, the apex more expanded than the base or the middle, 5–7 mm. long slightly before anthesis, lightly stellate-

[35] The identity of this species is based on the interpretation of Fawcett & Rendle in Jour. Bot. 59:224. 1921.

pubescent to glabrescent without, brownish and glabrescent within; petals yellow to brown, broadly obovate, about 5 mm. long and 2–3 mm. wide, the claw 1–2 mm. long, densely plumose; gonophore very short, less than 0.5 mm. long, the glands oblong, very small; urceolus short, deeply many-lobed, briefly ciliate; stamens 10–15, the filaments glabrous with 4–6 rows of retrorse serrations; ovary orbicular, about 1 mm. long, the spinules numerous, recurved, the style 5–6 mm. long, the stigma acute. Fruits small, orbicular, in dense nodose clusters, the body about 3–4 mm. in diameter at maturity, densely cinereous-tomentose, 3-loculate, each cell 1-seeded, the spines numerous, 75–100, about 1.0–1.5 mm. long, glabrous or nearly so; seeds ovoid, about 1.5 mm. long and 1.0–1.5 mm. wide.

A common weedy species of lowland tropics of both hemispheres, but apparently very rare on the continent of North America. Found in Florida and British Honduras where introduced. Flowers and fruits from July to November.

The small round fruits with dense cinereous tomentum between the short glabrous spines and the younger floral buds with very deeply cucullate sepals are constant characters throughout its wide range.

U. S. A.: FLORIDA: Sumter Co., Webster, *Curtiss 6738* (Mo).
BRITISH HONDURAS: Stann Creek, *Schipp 833* (Mo).
JAMAICA: *Swartz s. n.* (S).
HAITI: presqu'ile du Nord-ouest, *Ekman H9663* (S).
DOMINICAN REPUBLIC: Moncion, Prov. Monte Cristi, alt. 375 m., *Valeur 411* (NY, S),
PUERTO RICO: prope Mayaguez ad Guanajibo, *Sintenis 17* (C, S), *17c* (S); Coamo, *Sintenis 3134* (S).
VIRGIN ISLANDS: SAINT THOMAS: *Holton s. n.* (NY). SAINT CROIX: *Ricksecker 136b* (FM); Bassin yard, *Ricksecker s. n.* (NY); *Benzon 214* (C).
MARTINIQUE: *Duss 1364* (Mo); *Sieber 130* (Mo).
TOBAGO: Highmoor, *Broadway 3092* (Mo, S, U); near Frenchfield, *Egger 5633* (S); Dist. Les Coteaux, *Broadway 9071* (Mo).
TRINIDAD: Icacos, *R. O. Williams 10840* (TRIN); *Sieber 150* (G, Mo).
COLOMBIA: MAGDALENA: Santa Marta, Minca, *Engstedt 61* (S).
VENEZUELA: BOLIVAR: Ciudad Bolivar, alt. 35 m., *Holt & Gehriger 158* (US).
FRENCH GUIANA: vicinity of Cayenne, *Broadway 559* (US).
BRAZIL: AMAZONAS: Rio Negro, *Ule 8916* (S, US). BAHIA: Corcovado, antigua estrada, *Glaziou 1148* (BR, C, R); Andaarahy, porto de Tijuca, *Glaziou 8274* (R); vicinity Bahia, *Rose & Russell 19638* (NY, US), *Blanchet 188, 410* (G), *1285B* (BR, P), *s. n.* (Mo); exact locality lacking, *Salzmann 76* (G), *Martius 1263* (BR, G_a NY), *1265* (BR); *Glocker 1* (US). DISTRITO FEDERAL: Ilha de Taboinha, Guanabara, *Vidal s. n.* (R); exact locality lacking, *Lutz s. n.* (R); *Lima s. n.* (R). GOYAZ: Porto Imperial, *Burchell 8747* (BR). MATO GROSSO: Santa Anna da Chapadas, *Malme 3407* (S). MINAS GERAIS: Jard. Bot. Belo Horizonte, *Barreto 7925* (R); Fazienda da Chicaca, Munic. Santa Luzia, alt. 1100 m., *Assis 69* (US). PARÁ: Boa Vista on the Tapajoz River, *da Costa 151* (US). PERNAMBUCO: Tapéra, *Pickel 3278* (US). RIO DE JANIERO: Lünd ad Rio de Janeiro, *Warming 1270* (C); Engenhoça, *Warming 1241, 1255, 1259* (C); Atafona, *Sampaio 8142, 8991, s. n.* (R); estrada de Rodagem, Mericá, *Vidal s. n.* (R); Campo Bello, Carrapicho, *Sampaio 4624* (R); Vermelha, *da Costa 50114* (R); Campos, *Sampaio 50117* (R); Caxias, *Passarelli s. n.* (R); prope Rio, *Luschnath s. n.* (S); environs de Rio Janeiro, *Wedel s. n.* (BR); montagne des Orgues, alt. 800 m., *Wagner s. n.* (BR); prope Río-Janeiro, *Burchell 2939* (BR, P); exact locality lacking, *Houllet s. n.* (BR); *Meyen s. n.* (BR); *Lehmann s. n.* (BR); *Burchell 1043* (BR); *Glaziou 667, s. n.* (BR); *Anderson s. n.* (S); *Dusén 77* (S); *Valentin s. n.* (S); *Gartner 14* (US). SÃO PAULO: Campinas, *Heiner s. n.* (S); Santos, *Valentin s. n.* (S). DATA INCOMPLETE: *Alfont s. n.* (S);

Blanchet s. n. (G); *Cordoso s. n.* (R); *Gaudichaud s. n.* (P); *Kiedel 108, 110* (C, S); *Poblius s. n.* (BR); *St. Hilaire s. n.* (BR); *Widgren 534* (S).

PERU: LORETO: Iquitos, alt. 100 m., *Killip & Smith 27229* (US); Punchana, near Iquitos, *L. Williams 1314* (US).

40. TRIUMFETTA SAMPAIOI Monteiro, in Lilloa 3:244. 1938. (T.: *da Costa 65A*).

Shrubs 1–2 m. high; branches and inflorescence axes terete, with few long, stellate and simple hairs. Leaves broadly ovate to deeply 3-lobed, about 9 cm. long and 3 cm. wide, the base cuneate to obtuse, the tip gradually and narrowly acuminate, regularly and doubly serrate, both surfaces with few long, stellate and simple hairs, especially on the veins; petioles about 3 cm. long, densely clothed with long hairs. Inflorescences axillary, the cymes of 4 cymules, condensed in the axils of the bracts, the flowering peduncles about 4 mm. long, the pedicels 1–2 mm. long. Flowers hermaphrodite, the buds oblongoid, small, about 3 mm. long slightly before anthesis, apical appendages prominent though short; sepals oblong, deeply cucullate in younger buds, about 3.5 mm. long, pilose without, glabrescent within; petals narrowly obovate, subequalling the sepals, the claw about 1.5 mm. long, very lightly plumose; gonophore about 0.75 mm. long, the glands quadrangular, small; urceolus absent; stamens 5, the filaments with 4 rows of retrorse serrations, pubescent at the base; ovary orbicular, about 1 mm. long, the spinules about 50, recurved, the style 3–4 mm. long, the stigma very briefly 3-parted. Fruit suborbicular, small, in dense nodose clusters, the body about 3 mm. in diameter at maturity, rather densely long-tomentose, 3-loculate, each cell 1-seeded, the spines 30–50, about 1 mm. long, plumose; seeds pyriform, small.

Known only from northeastern Brazil; flowering and fruiting from March to June.

BRAZIL: CEARA: Maracanahú, Est. Exp. de Pl. Texteis em S. Antonio, *Rodriguez 26* (R); Crato in Caapuerao, *Löfgren 619* (S); exact locality lacking, *Rocha 25* (R). MARANHÃO: Island of São Luiz, *Fröes 11884* (US). PARA: Río Murucutu, Belem, *da Costa 65A* (R); Belem, Carrapicho, *Silva s. n.* (US).

This species is very closely related to *T. Bartramia*, and the superficial resemblance is rather striking. However, the absence of the urceolus, the presence of only 5 stamens, and the plumose spines differentiate it sufficiently.

41. TRIUMFETTA PANICULATA Hook. & Arn. Bot. Beechey Voy. 279. 1841. (T.: *Beechey Herb. s. n.* in Herb. Kew.).

Heliocarpus tigrinus Hochr. in Ann. Conserv. Jard. Bot. Genève 18:123. 1914. (T.: *Langlassé 708*).
Triumfetta tigrina (Hochr.) Standl. in Contr. U. S. Nat. Herb. 23:1674. 1926.
Triumfetta leiocarpa Standl. in Field Mus. Publ. Bot. 11:167. 1936. (T.: *Emrick 130*).
Triumfetta Matudai Lundell, in Contr. Univ. Mich. Herb. 7:27. 1942. (T.: *Matuda 2148*).

Small trees or shrubs 3–5 m. high; older branches glabrous, generally angled with decurrent petiole bases, the younger stems and inflorescence axes longitudinally ridged, clothed with short separate tufts of stellate hairs. Leaves broadly ovate, profoundly 3- to 5-lobed, about 15–18 cm. long and 16–20

cm. wide, lightly pubescent, usually scabrous, the veins densely tomentose; petioles 4–7 cm. long, coarsely stellate-pubescent. Inflorescences terminal, the cymes of 3–5 cymules, usually in dense nodose clusters, the flowering peduncles 3–5 mm. long, the pedicels 2–5 mm. long. Flowers hermaphrodite, the buds obovoid, 5–7 mm. long and about 3 mm. wide slightly before anthesis, constricted towards the base, the apical appendages short, nearly obsolete; sepals obovate, about 6 mm. long, with short rough stellate hairs without, glabrescent within; petals linear, yellow to brown, 3–4 mm. long, the claw about 1 mm. long, densely plumose; gonophore short, about 0.5 mm. long, the glands spherical to slightly elliptical, small; urceolus short, 0.25–0.50 mm. high, many-lobed, lightly ciliate; stamens 30–40, the filaments glabrous, smooth; ovary orbicular, about 1.5 mm. long, the spinules numerous, recurved, the style 2–3 mm. long, the stigma briefly 2-parted. Fruit globose, large, the body about 6 mm. in diameter at maturity, glabrous, 2-loculate, each cell 2-seeded, later falsely 4-celled, each with 1 seed, the spines numerous, glabrous, 3–5 mm. long; seeds ovoid, 2–3 mm. long and 1.5–2.5 mm. wide.

Western Mexico, usually growing in oak forests at altitudes of about 500 m.; flowering and fruiting from September to early December.

MEXICO: CHIAPAS: Escuintla, *Matuda 2148* (FM, MICH, NY). COLIMA: Coahuayana, *Emrick 130* (FM). GUERRERO: La Morena, alt. 450 m., *Langlassé 708* (G, GH); Vallecitos, Montes de Oca, *Hinton 11602* (GH). JALISCO: exact locality lacking, *Beechey Herb. s. n.* (K). SINALOA: Quebrado de Mansana, Sierra Surotato, alt. 4000–4500 ft., *Gentry 6507* (Mo); in the foothills of Sierra Madre, *Rose 1768* (US); San Ignacio, San Juan, *Ortega 6880* (FM); exact locality lacking, *Ortega 4768* (US).

Hooker and Arnott gave only a brief description of the spines and referred to three rather brief diagnoses by Schlechtendal[36] for the descriptions of the flowers and the habit. Schlechtendal's descriptions were based on plants collected by Schiede and Deppe. None of the descriptions are adequate, and because of this, *T. paniculata* has been little known in the herbarium. The decurrent petiole bases on the stems, the large, usually 3- to 5-lobed glabrous leaves, the small obovoid floral buds, and the relatively large glabrate fruits, characterize this species. The ebracteolate, terminal inflorescence tends to confuse this species with the genus *Heliocarpus*.

42. TRIUMFETTA GALEOTTIANA Turcz. in Bull. Soc. Nat. Moscou 32[1]:260. 1859. (T.: *Galeotti 4153*).

Triumfetta apetala Hochr. in Ann. Conserv. Jard. Bot. Genève 18:97. 1914. (T.: *Galeotti 4152*).

Shrubs 2–3 m. high; branches and inflorescence axes scurfy, coarsely stellate-tomentose. Leaves broadly ovate to 3-lobed, 7–12 cm. long and 4–8 cm. wide, sometimes slightly larger, the base rounded or subcordate, the tip gradually and narrowly acuminate, the serrations irregular, acute, the basal ones generally glandular, both surfaces scabrous, clothed lightly with many short tufts of stellate hairs,

[36] Schlecht. in Linnaea 5:288. 1830; 6:424. 1831; 11:376. 1836.

Fig. 13. *Triumfetta Galeottiana*

the veins densely tomentose; petioles 3–5 cm. long, coarsely stellate-pubescent. Inflorescences gynodioecious, axillary, rarely terminal, hermaphrodite, large and spreading, the cymes of 3–5 cymules, usually in dense nodose clusters, the flowering peduncles 3–5 mm. long, the pedicels 2–4 mm. long, the buds obovoid, 5–7 mm. long and about 3 mm. wide slightly before anthesis, constricted towards the base, the apical appendages short, nearly obsolete, the sepals obovate, about 6 mm. long, with short rough stellate hairs without, glabrescent within, the petals linear, yellow to brown, 3–4 mm. long, the claw about 1.5 mm. long, densely plumose,

the gonophore slender, 1.0–1.5 mm. long and about 0.75 mm. wide, the glands oblong, prominent, the urceolus about 0.5 mm. high, many-lobed, densely ciliate, the stamens 20–30, the filaments retrorsely 2-serrate, the ovary ovoid, about 1 mm. long, the spinules about 50, recurved, the style less than twice the length of the ovary, the stigma very briefly 3-parted; pistillate inflorescence of the same general nature and size as the hermaphroditic one, the buds oblongoid, about 3–4 mm. long slightly before anthesis, the apical appendages nearly obsolete, the sepals 3–5 mm. long, with short separate tufts of stellate hairs without, glabrescent within, the petals absent, the gonophore elongate, about 1.5 mm. long, the glands oblong, prominent, the urceolus about 0.5 mm. high, many-lobed, densely ciliate, the staminodes 15–20, about 2 mm. long, the ovary orbicular, the spinules about 50, the style about twice the length of the ovary, the stigma very briefly 3-parted. Fruit globose or subglobose, the body glabrous, 3–4 mm. in diameter at maturity, 3-loculate, each cell 1-seeded, the spines 30–40, each 3–4 mm. long, straight, glabrous; seeds pyriform, 1.5–2.0 mm. long and about 1.5 mm. wide.

Southern Mexico, in dry sunny places at altitudes of 500 to 2000 m.; flowering in September and October, the fruit maturing from late October to middle of December.

MEXICO: GUERRERO: Mancho, Mina, alt. 1200 m., *Hinton 9641, 9642, 9643, 9644, 9670* (GH); Zihuagio, Mina, alt. 1100 m., *Hinton 9720* (GH); Río Frio, Mina, alt. 1300 m., *Hinton 10717* (Mo, US), *10718* (GH); Pilas, Mina, alt. 1600 m., *Hinton 10744* (US); Carrizo-Sto. Domingo, Galeana, alt. 1200 m., *Hinton 14371, 14638* (GH); between Petatlan and Chilapa, alt. 5000–6500 ft., *Nelson 2155* (US); San Geronimo, *Altamirano 659* (US). JALISCO: near Etzatlan, *Rose & Painter 7520* (NY, US); between Atequiza and Chapala, *Rose & Painter 7609* (US). MÉXICO: Distr. Temascaltépec: Carboneras, alt. 2000 m., *Hinton 1857* (Mo), *5077, 6827* (US); Ixtapan, alt. 1000 m., *Hinton 2278* (US); Nanchititla, *Hinton 5249* (US); Las Mesas, *6415, 6784* (Mo, US); Tejupiko, *Hinton 6777* (Mo). MICHOACAN: vicinity of Morelia: Coronilla, alt. 1900 m., *Arsène 2540* (Mo, US); Loma Sta. Maria, alt. 1950 m., *Arsène 2978* (GH, Mo, US), *5879* (GH, Mo, NY, US), *7281* (US); Coalcomán, Salitro-Mesa, alt. 1800 m., *Hinton 12484, 12485* (US); Zitacuaro, alt. 1400 m., *Hinton 13340* (GH, Mo); south of Torricillas, *Hinton 15281* (GH, US); Tancitaro, Uruapan, *Hinton 15681* (GH). NAYARIT: road from Tepic to Los Aguacates, alt. 1000 m., *Mexia 583a* (US); trail from Tepic to Santiago, alt. 1000 m., *Mexia 639* (Mo, US). OAXACA: Cerro de San Felipe, 1900 m., *Conzatti 453* (US), *1617* (NY, US); Valley of Etla, *Alvarez 728* (GH, US); Zinatlan, alt. 1925 m., *Conzatti & Velde 4676* (BR); exact locality lacking, *Moricand s. n.* (G). SINALOA: Las Mesas, Sierra Surotato, alt. 3000 ft., *Gentry 6142* (Mo); Quebrado de Mansana, Sierra Surotato, alt. 4000–5000 ft., *Gentry 6454, 6454a, 6454b, 6454c, 6561* (Mo). VERA CRUZ: Zacuapan, Cordillera, alt. 3000 ft., *Galeotti 4152* (BR), *4153* (BR, G, US); Orizaba, *Botteri s. n.* (GH), *765* (G, P), *988* (P), *1110* (GH, US); above Orizaba, *Smyth 162* (US); *Müller s. n., 543* (NY), *148* (BR, NY); Zacuapan and vicinity, Barranca de Tenampa, *Purpus 2109, 3661* (Mo, US), *3058* (Mo, NY, UC, US); Mirador, *Liebmann 532* (US); Totutla, *Liebmann 509* (US). DATA INCOMPLETE: *Mohr s. n.* (US); *Linden Suppl. 47* (BR).

Triumfetta apetala has been treated thus far as a distinct species. I am convinced that it is the pistillate form of *T. Galeottiana*, as the younger fruiting specimens can be assigned to *T. Galeottiana* despite the fact that they have apetalous, pistillate flowers. I do not know of any mature fruiting specimen that could be included in *T. apetala* in opposition to *T. Galeottiana*.

43. TRIUMFETTA HELIOCARPOIDES Bullock, in Kew Bull. 293. 1937. (T.: *Hinton 5159*).

Small shrubs 1.0–1.5 m. high; branches and inflorescence axes minutely stellate-tomentose. Leaves broadly ovate, usually 3-lobed, 10–15 cm. long and 7–9 cm. wide, the base subcordate to rounded, the tip gradually and narrowly acuminate, rather regularly and doubly serrate, the upper surface green, scabrous, very lightly pubescent with minute tufts of stellate hairs, the lower pallid, slightly more pubescent with prominent veins and veinlets; petioles long and slender, 5–10 cm. long, with short separate tufts of stellate hairs. Inflorescences gynodioecious, pistillate terminal, the cymes of 4–6 cymules, condensed in dense nodose clusters, the flowering peduncles 3–4 mm. long, the pedicels about 2 mm. long; flowers small, the bud about 3 mm. long slightly before anthesis, the apical appendages prominent though short; sepals oblong, 3–4 mm. long, densely but minutely tomentose without, glabrescent within; petals obovate, very small, only about 1 mm. long, the claw lightly plumose; gonophore 0.5–0.75 mm. long, the glands oblong, small, with ciliate upper margins; urceolus short, many-lobed, distinctly ciliate; staminodes 10, about 2 mm. long; ovary orbicular, the spinules about 25, recurved, the style about 1.5 mm. long, the stigma briefly 2-fid; hermaphroditic inflorescence not seen. Fruit orbicular, the body about 2 mm. in diameter at maturity, dark brown to black, glabrous, 3-loculate, usually 1 cell aborted, each 1-seeded, the spines 20–25, glabrous, 3–4 mm. long; seeds pyriform, small.

Known only from the state of México, usually growing at an altitude of about 1000 m.; flowering and fruiting from October to November.

MEXICO: MÉXICO: Ixtapan, Temascaltépec, alt. 1000 m., *Hinton 5159* (K, NY), *7001* (GH, K); Tejupilco, *Hinton 6779, 6780* (K).

DOUBTFUL SPECIES

1. TRIUMFETTA CALYCINA Turcz. in Bull. Soc. Nat. Moscou 36^1:574. 1863. (T.: Peru, *Mathews 889*).

A large-flowered species allied either to *T. speciosa* or *T. mollissima*. I have not seen the type, but the description fits *T. multilocularis*, except for the fact that *T. calycina* reportedly has only 15–16 stamens, whereas *T. mollissima* has 25–30.

2. TRIUMFETTA JELSKII Szysz. in Rozpr. Akad. Umiejet. [Krakow], Mat.-przy. II, 9:224. 1895. (T.: Tambillo, Peru, *Jelski 280*).

A species allied to *T. caudata* according to the description. I have not seen the type and the description is inadequate for diagnosis.

3. TRIUMFETTA BRACHYPETALA Urb. & Ekm. in Arkiv f. Bot. $23A^5$:80. 1930. (T.: Haiti, *Ekman H. 9462*).

A hybrid species between *T. Lappula* and *T. semitriloba*. I have not seen the type, and the very short description is inadequate for diagnosis.

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MISCELLANEA TAXONOMICA. I.

GRAMINEAE

SPOROBOLUS **hians** G. B. Van Schaack spec. nov. Gramen perenne usque ad 50 cm. altum. Culmi laxe fasciculati erecti 5–6-nodes, internodiis inferioribus brevissimis summo elongato et demum exserto. Foliorum inferiorum vaginae breves imbricatae valde striatae margine antrorse ciliato et ad apicem lateraliter barbatae caeterumque glabrae, summa glabra margine sparse pilosulo excepto; ligula ad seriem ciliorum usque ad .5 mm. longorum redacta; laminae inferiores planae 2–3 mm. latae usque ad 7 cm. longae in apicem tenuiter acutum gradatim attenuatae subtus laeves supra et margine scabridulae, superiores non visi. Panicula anguste pyramidalis usque ad 20 cm. longa et 10 cm. lata; rhachis gracilis inferne laevis superne antrorse minuteque scabra; rami praecipui capillares paullo flexuosi laeves vel minute scabri plerumque solitarii horizontaliter patentes, secundarii capillares patentes laxe spiculati; pedicelli laeves 1–3 mm. longi, terminali 3–5 mm. longo. Spiculae lanceolatae acutae 1.6–1.8 mm. longae in antheso hiantes purpureo-suffultae. Gluma inferior lanceolata .8 mm. longa obtusa erosa enervis hyalina, superior anguste ovata .9–1.0 mm. longa truncata erosa hyalina enervisque vel 1-nervis. Lemma lanceolatum vel ovatum 1.5–1.7 mm. longum acutum 1-nerve. Palea lemmati aequilonga acuta marginibus hyalinis. Antherae 1 mm. longae. Caryopsis non visus.—BRAZIL: MINAS GERAIS: S. Terezinha, Municipio Ituiutaba, Dec. 20, 1949, *A. Macedo 2045*. "Grass from 'Resfriado'." (Herb. Missouri Bot. Gard., HOLOTYPE).

Sporobolus hians resembles S. *pseudairoides* Parodi but differs from it in having shorter leaves, spreading panicle branches, a palea equalling the lemma in length and anthers 1 mm. long, the latter species having anthers only .25 mm. long.

LILIACEAE

HERRERIA **latifolia** Woodson, spec. nov. Frutex volubilis ramulis glabris glaucis sparse irregulariterque aculeolatis, internodiis ca. 15–18 cm. longis 2–3 mm. diametralis nodis incrassatis. Folia in rosulis oppositis sessilibus 6–7 sessilia obovato-elliptica apice breviter acuminata basim ca. tertia parte superiore versus gradatim angustata inter se plus minusve inaequalia 9–15 cm. longa 3–5 cm. lata membranacea utrinque glabra crebre multinervia. Inflorescentia per quamque rosulam unica paniculata vel pauciramosa 15–30 cm. longa, multiflora pedunculo glauco minute denseque hirtello vel basi glabrato; floribus luteolis, pedicellis ca. 2–3 mm. longis minute hirtellis, bracteis subtendentibus ovato-aculeatis subaequantibus, tepalis oblongo-ellipticis 3.5 mm. longis 2 mm. latis subaequalibus apice late acutis ibique minute papillatis caeterumque glabris basi in tubo campanuliformi ca. 1 mm. longo coalitis, filamentis staminum aciculiformibus 1.5 mm. longis glabris, antheris compresse ellipsoideis basi usque ad medium fissis 1.5 mm. longis, pistillo ampuliformi 3.5 mm. longo glabro.—BRAZIL: MINAS GERAIS: voluvel dos terrenos de pedra, S. Terezinha, Municipio Ituiutaba, Nov. 26, 1949, *A. Macedo 1317* (Herb. Missouri Bot. Gard., HOLOTYPE).

Issued September 30, 1950.

This certainly is the most handsome species of *Herreria* known at the present time. It is apparently most closely related to *H. Glaziovii* H. Lec. (*Glaziou 14,354* in hbb. Copenhagen and Missouri Bot. Gard.), which, however, has verticillate leaf-rosettes and clustered inflorescences with shorter, more branched, and glabrous peduncles.

VELLOZIACEAE

VELLOZIA **Macedonis** Woodson, spec. nov. Suffrutex subcaespitosus. Caudex subnullus simplex vel dichotome divisus foliorum emortuorum reliquiis tectus. Folia subradicalia lineari-aciculiformia 5–10 cm. longa medio ca. 2 mm. lata apicem obtusem gradatim attenuata basim versus gradatim ampliata vagina hyalina ca. 6 mm. longa 3 mm. lata fulvescentia margine proximate setoso-aculeolata caeterumque glabra multinervosa. Flores solitarii terminali longe pedunculati; pedunculo 6–8 cm. longo 3-gono 6-costato glabro; germine conico-campanulato indistincte 3-gono ca. 7 mm. longo, ostio ca. 5 mm. lato stramineo glabro laevi vernicoso margine obscure lobato; tepalis violaceis 6 oblongo-ellipticis acutis ca. 1 cm. longis 4–5 mm. latis; staminibus 18 in fasciculis 6 triplice convenitis, fasciculis tubo perianthii adnatis obtriangularibus tenuibus glabris exappendiculatis, filamentis et antheris subaequilongis sed medio in fasciculo paulo altius inserto cunctis ca. 5 mm. longis; stylo ca. 1 cm. longo, stigmate depresso-globoso ca. 1.5 mm. lato.—BRAZIL: MINAS GERAIS: mountains, alt. 1200 m., Ouro Preto, Jan. 7, 1950, *A. Macedo 2072* (Herb. Missouri Bot. Gard., HOLOTYPE).

The habit of this species is reminiscent of *V. caruncularis*, although, of course, the latter has a densely tuberculate hypanthium. Our species appears to be most related to *V. graminea* Pohl, which, however, has strongly unequal stamens and elaborately appendaged phalanges.

LEGUMINOSAE

PITHECOLOBIUM **steyermarkii** Schery, spec. nov. Sect. CAULANTHON. Arbor ramulis juventate brunneo-tomentulosis, prominente lenticellatis. Folia magna, pinniis 2-jugatis; petiolis brunneo-tomentulosis teretibus ca. 4 cm. longis, rhachibus aequalibus glande crateriforme sessile inter insertionem pinnarum inferiorum, rhachibus secondariis eglandulosis; foliolis oppositis 3–5-jugatis et una solitaria addita base extus, ovato-lanceolatis 4–8 cm. longis 15–30 mm. latis apice acuminatis basi late acutis, subtus leviter brunneo-tomentosis nervis prominentibus, supra glabris fuscioribus reticulatis; stipulis lanceolatis ca. 4 mm. longis. Inflorescentiae subfasciculatae cauliflorae brevi-spicate; floribus albis fragrantissimis sessilibus congestis subcapitatis, pedunculis 5–8 cm. longis brunneo-pubescentibus, bracteis ovatis parvis 1 mm. longis; calycibus cupuliformibus ca. 2 mm. longis brunneo-tomentosis brevi-dentatis, corollis tubulari-infundibuliformibus 8–9 mm. longis brunneo-tomentulosis brevi 5-dentatis, staminibus multis ca. 18 mm. longis tubo brevi exserto, ovariis lineari-oblongis, glabris, multiovulatis; fructu ignoto.—ECUADOR: Prov. Santiago-Zamora, along Quebrada Honda, vicinity of Rancho Achupallas, alt. 2500–2700 m., *J. A. Steyermark* (Herb. Missouri Bot. Gard. TYPE).

Pithecolobium steyermarkii

A tree with twigs, rachises and inflorescence brown-tomentulose; the leaves large, bipinnate, the pinnae 2 pairs and the leaflets 3–5 pairs plus a single basal leaflet to the outside on each pinna; the ovate-lanceolate leaflets opposite, short-petiolulate, relatively large (4–8 cm. long), pubescent (especially on veins) and light brown below, glabrous, darker and somewhat lustrous above; with 4 or 5 very prominent strongly arcuate lateral veins more or less confluent apexward a mm. or so from the margins, numerous smaller secondary and tertiary veins reticulate, the petiole bearing a single crateriform gland between insertion of the lower pinna pair, but it, the rachis and secondary axes otherwise eglandular. The congested or subfasciculate inflorescenses are borne on short spurs from the woody trunk; they are long-pedunculate, the floriferous portion very short-spicate (ca. 5 mm.) and thus appearing subcapitate. The congested, sessile, white flowers are described as very fragrant; the pubescent corolla is 4 to 5 times the length of the cupulate calyx, its teeth lanceolate, 1–2 mm. long, the tube about 7 mm. long; the ovary is turgid, symmetrical, glabrous.

The outstanding features of *P. steyermarkii* are the 2-jugate pinnae with relatively few and large leaflets, and the cauliflorous pedunculate inflorescences. A related species is apparently *P. ramiflorum* Benth., of Brazil, which, however, is said to have sessile spikes and larger leaflets.

ALBIZZIA **paucipinnata** Schery, spec. nov. Arbor 15 m. ramulis glabris longitudinaliter rugosis inconspicue lenticellatis. Folia magna bipinnata, pinnis 3–5-jugatis suboppositis; petiolis 3–5 cm. longis glabris supra subsulcatis glande parva conica vel subcrateriforme versus basem, rhachibus ca. 6–7 cm. supra sulcatis puberulis, axibus pinnarum ca. 6–8 cm. eglandularibus supra sulcatis puberulis; foliolis 7–12-jugatis oppositis inaequilateraliter oblongis 1–2 cm. longis 5–9 mm. latis, sessilibus, basi oblique rotundato-truncatis apice rotundatis et minute apiculatis, subtus puberulis supra glabris nitidis, costa aliquantum excentrica venis secondariis 3–4 paribus ascendentibus; stipulis nullis. Inflorescentiae terminales et subterminales axillares foliis aequilongae (ad 15 cm.) nodosae racemosae capitulis fasciculatis pedunculatis, pedunculis 1–pauci-aggregatis ca. 1 cm. longis tomentulosis, capitulis ca. 1 cm. diametro, bracteis lanceolato-cucullatis parvis pubescentibus; floribus albis odoratis multis congestis sessilibus, calycibus infundibuliformibus paene 2 mm. longis breviter et late 5-lobatis leviter puberulis, corollis infundibuliformibus ca. 3–4 mm. longis apice puberulis lobis ovate-lanceolatis prominentibus, staminibus multis (ca. 18) ca. 7 mm. longis tubo incluso, ovariis oblongis glabris turgidis multi-ovulatis; fructibus ignotis.—ECUADOR: Prov. El Oro, along Rio Amarillo upstream from Portovelo, alt. 640–760 m., *J. A. Steyermark 54035* (Herb. Missouri Bot. Gard. TYPE).

A large tree, the leaves bipinnate with few (3–5) pairs of subopposite pinnae, the pinnae with about 9 pairs of modest, sessile leaflets; the glabrous petiole moderately elongate and bearing a sessile gland basally, slightly exceeded by the eglandular rachis which is puberulent along the top side; leaflets inequilaterally oblong with a tendency toward being subfalcate, but rounded and minutely mucronulate apically, subtruncate basally, glabrous and lustrous above, puberulent below, the costa excentric but not marginal, the few lateral veins markedly ascending. The inflorescences arise from the upper axils as elongate nodose racemes of pedunculate heads that occur fasciculate from the rachial nodes; the peduncles are little more than 1 cm. long the heads (when dry) about 1 cm. in diameter. Flowers are small, funnelform, the corolla lobed for about 1/3 its length and about twice as long as the calyx; the staminal tube is included but about equalling the corolla.

The species is related to *Pithecolobium (Samanea) coripatense* Rusby [ALBIZZIA **coripatense** (Rusby) Schery n. comb.], from which it differs in being more glabrous, with somewhat longer flowers and inflorescences, and without glands on the pinnular rachis; and to *P. (Samanea) multiflorum* (HBK.) Benth., from which it differs in not having the leaflets falcate, glabrous, acute.

Cyathostegia (Benth.) Schery, gen. nov.

Swartzia, Sect. CYATHOSTEGIA Benth. in Benth. & Hook. Gen. Pl. 1:561. 1865.

Frutices *Swartziae* similes, calycibus cyathiformibus numquam irregulariter ruptis, leguminibus planis submembranaceis, bracteis persistentibus vel subpersistentibus, ovariis 1–2-ovulatis.

In working over Steyermark's Ecuadorean Leguminosae, Nos. 54839 and 54840, cursorily indicated by Dr. Steyermark as *Ateleia* (PAPILIONOIDEAE, SOPHOREAE), proved to belong to the section CYATHOSTEGIA of the genus *Swartzia* (CAESALPINOIDEAE, SWARTZIEAE). As nearly as can be told "ex char." they fall within the concept of *S. weberbaueri* Harms (in Fedde Rep. Sp. Nov. 18:235. 1922.). A check through the herbarium and literature on *Swartzia* made it apparent that both *S. mathewsii* Benth. (in Hook. Icon. III, 1:51, *pl. 1064.* 1870) and *S. weberbaueri*, apparently the only species of the section CYATHOSTEGIA, are quite untypical of *Swartzia*, and their inclusion there both inconvenient and misleading. It is therefore proposed to elevate the section CYATHOSTEGIA to generic rank, to become the genus *Cyathostegia* (CAESALPINOIDEAE, SWARTZIEAE) transitional from the CAESALPINOIDEAE to the SOPHOREAE of the PAPILIONOIDEAE. As such the genus is confined, as far as is known, to the Andean area of Brazil, Ecuador, Peru and probably Bolivia.

This genus is characterized, as is usually *Swartzia*, by unipetiolate flowers; many (about 30) stamens free or barely united at the base, the inner ones somewhat more slender and shorter, with large linear-oblong anthers; stiped ovary and (dehiscent) fruit; and slender style with small terminal stigma. However, the calyx is distinctly cyathiform or cupulate, subtruncate apically, not rupturing irregularly; the legume is flat and thin, never fleshy or turgid, one-seeded, exarillate, the valves thin and submembranous; the ovary is 1 to 2-ovulate, in contrast to the usually pluri-ovulate ovary characteristic of *Swartzia;* the bracts and bractlets are relatively persistent in contrast to the "very caducous" characterization of *Swartzia;* the stipe of the ovary is briefly adnate to the cupulate calyx below insertion of the petal and stamens; and the leaflets are more numerous than is often the case in *Swartzia*.

The species thus become **Cyathostegia matthewsii** (Benth.) Schery, n. comb. and **C. weberbaueri** (Harms) Schery, n. comb. The latter can be distinguished from the former by the longer, more lax inflorescense, the larger flowers and the smaller leaves. In *Steyermark 54839* the 1–3 lower flowers of the raceme that are in anthesis are strikingly larger than the several buds higher on the rachis. Both the large flowers and the small buds seem to be perfect and complete (although the style is not very evident in the buds), but the superficial appearance is that of a few perfect flowers below with staminate flowers above.

CASSIA **vargasi** Schery, spec. nov. Arbor?, ramulis flavo-tomentosis longitudinaliter substriatis, internodiis ca. 6 cm. longis. Folia magna 10–12-foliolata, stipulis ovato-lanceolatis ca. 7 mm. longis; petiolis ca. 2 cm. longis tomentosis

eglandularibus, rhachibus ca. 10 cm. longis flavo-tomentosis glande conico interpetiolulari inter jugem inferiorem foliolorum et frequenter inter alia juga; foliolis ovatis vel ellipticis, 2.5 (inferioribus)–8 (superioribus) cm. longis, 2–3 cm. latis apice late acutis base obtusis supra leviter pubescentibus subtus flavo-tomentosis, venis lateralibus ca. 8–10 paribus. Inflorescentia racemosa axillaris ca. 10 cm. longa; pedunculis ca. 7 cm. longis tomentosis; bracteis ovato-lanceolatis ca. 8 mm. longis subpersistentibus flavo-tomentosis; floribus aggregatis, pedicellis inferioribus ca. 3 cm. longis; sepalis inaequalibus ovatis vel orbiculari-oblongis 7–14 mm. longis longitudinaliter venosis glabris vel subglabris; petalis orbicularibus fere aequimagnis ca. 2 cm. longis conspicue venosis flavis glabris; staminibus 7, staminodiis 3, 4 antheris brevioribus ca. 6 mm. longis brevi-rostratis, filamentis 2–3 mm. longis, 3 antheris longioribus 7–9 mm. longis, filamentis 7–8 mm. longis fere erostratis; ovario lineari tomentoso stipitato turgido, stylo glabro, stigmate parvo; legumine ignoto.—Peru: cuzco: Prov. Urubamba, Machupicchu, Feb., 1938, *C. Vargas C 985* (Herb. Missouri Bot Gard., holotype).

By inference small tree or coarse shrub, yellow-tomentose throughout (older branchlets not seen); leaves large, 10- to 12-foliolate, the petiole and rachis markedly yellow-tomentose, bearing a black conic gland about 1 mm. long between the lower pair of leaflets and frequently the other pairs of leaflets as well; lower leaflets usually ovate and only ½ to ⅓ as long as the generally elliptic terminal leaflets, pubescent above and below, more heavily so (tomentose) and lighter in color below; inflorescence a long-pedunculate axillary raceme nearly equalling the leaf rachis, floriferous for about the terminal ¼ of its length, the conspicuous yellow-tomentose bracts subpersistent; pedicels of mature (lower) flowers elongate, the unopened buds (apexward) congested and sessile near the tip; sepals from the outermost inward becoming larger and more petaloid, essentially glabrous except the outermost lightly pubescent; petals large, short-clawed, glabrous, conspicuously venose; fertile stamens 7, glabrous, opening by paired but confluent terminal pores, the lowermost with a comparatively thin, elongate filament and a nearly erostrate, scarcely sagittate anther, the 2 median ones similar but with thicker, margined filaments and slightly larger anthers, the 4 upper ones with short, thick filaments and smaller, briefly rostrate anthers; staminodia 3–4 mm. long, obovate, flat, thin, the "blade" equalling the "claw"; ovary cinereous-tomentose, the style glabrous, the stigma terminal and inconspicuous.

This species falls near the well-known *Cassia (Adipera) tomentosa* L. f., from which it seems worthy of separation on the basis of the larger proportions in general, and the fewer and much larger leaflets. Possibly it grades into *Adipera santanderensis* Br. & Killip of Colombia, another variant of the *C. tomentosa* complex, but bears 5–6 rather than 4–5 pairs of leaflets and is decidedly more pubescent.

Galactia **pedunculata** Schery, spec. nov. Herba perennis subvolubilis tenuissima semiprostrata ca. 4 dm. longa, xylopodo ignoto sed ut videtur crassato; caulibus teretibus flexuosis subglabris vel minutissime appresso-strigillosis. Folia trifoliolata; stipulis anguste lanceolatis ca. 1.5 mm. longis; petiolis ca. 25 mm.

longis minute appresso-pubescentibus eglandularibus; foliolis linearibus 20–50 mm. longis et 3–6 mm. latis ad apicem obtusem angustatis ad basem rotundatis vel subcordatis supra glabris subtus leviter minuteque aureo-strigillosis et minutissime cinereo-lepidotis, venis lateralibus confluentibus prominente reticulatis, marginibus revolutis, petiolulis brevibus puberulentis, stipellis subulatis 1–1.5 mm. longis. Inflorescentia axillaris racemosa, pedunculis ca. 45 mm. longis; floribus paucis (ca. 5) terminaliter aggregatis vel subumbellatis purpureis, bracteis lanceolatis ca. 1.5 cm. longis, pedicellis 1–3 mm. longis pubescentibus; calycibus 5–6 mm. longis usque tertio inferiore pentapartitis lobis plus minusve aequimagnis ovato-lanceolatis acutis extus leviter aureo-puberulentis, vexillis orbicularibus ca. 12 mm. longis emarginatis glabris ad basem biauriculatis breve-unguiculatis, alis et carinis aequilongis subspatulatis ad basem auriculatis, staminibus glabris vexillo ad medium concrescenti, ovario plano pubescenti usque 10–15-ovulato, stylo glabro, stigmate parvo; legumine ignoto.—BRAZIL: MINAS GERAIS: on rocky terrain at about 1200 m., Ouro Preto (Saramenha?), Jan. 7, 1950, *A. Macedo 2070* (Herb. Missouri Bot. Gard., HOLOTYPE).

Slender, half-prostrate, vine-like herb to several dm., apparently perennial from a thickened rootstock; stems flexuous, minutely appressed strigose or subglabrous in age; leaves trifoliolate, stipulate, prominently petiolate; leaflets linear (in a few first-formed, basal leaves linear-lanceolate), gradually contracted to a blunt and briefly mucronate apex, glabrous above, scatteringly golden-strigulose below and minutely cinereous-scurfy, the costa prominent, depressed above but elevated below, the lateral venation markedly reticulate; inflorescence a very contracted head-like or umbel-like axillary raceme (or condensed panicle?), floriferous for the upper few mm. with a few short-pedicellate flowers but conspicuously pedunculate below, the peduncle almost twice the length of the petioles; flowers moderate, the calyx prominently 5-lobed, the corolla about 12 mm. long; stamens equalling the corolla, fused for at least half their length, the alternate filaments somewhat unequal; anthers versatile, elliptic, less than 1 mm. long, with a dark connective; ovary linear, pubescent (especially marginally), flattened; style glabrous, arcuate, comparatively stout and terminating abruptly as an unexpanded, glabrous stigma.

This species is similar to *G. linearifolia* Hoehne, known from São Paulo, Brazil. It is one of a very few species centering around the rather unique *G. gracillima*. *G. pedunculata* differs from both *G. gracillima* and *G. linearifolia* in the conspicuously pedunculate inflorescences. The vine-like habit and unusual, slender leaflets serve to distinguish it from most other species of *Galactia*. The genus is regarded as generally having the vexillar stamen free. This is not true of *C. pedunculata* nor its near relatives.

VIOLACEAE

RINOREA **roureoides** Woodson, spec. nov. Arbor ca. 7 m. alta; ramulis graciliusculis glabris. Folia alternata obovato-elliptica subcaudato-acuminata basi obtusa vel late acuta apicem versus indistincte crenulata ca. 7–12 cm. longa ca.

2.5–5.0 cm. lata firmiter membranacea utrinque opaca glabra prominente venosa; petiolis ca. 5 mm. longis glabris. Inflorescentia paniculata in axillis foliorum superiorum fasciculata rariusve solitaria; pedunculis ca. 4–7 cm. longis gracilibus minute papillatis, ramulis inferioribus 3–5-floris superioribus saepissime 1-floris, bracteis minimis anguste lanceolatis. Flores albi; pedicellis ca. 2 mm. longis minute papillatis; calycis laciniis aequalibus ovato-deltoideis late obtusis 3-nerviis ca. 1 mm. longis minute ciliolatis; petalis late oblongis ca. 3 mm. longis ciliolatis; staminum filamentis ca. 1 mm. longis basi glandula reniformi minute emarginata ca. 0.5 mm. longa adnata, antheris subquadratis ca. 0.5 mm. longis, appendicibus apicalibus latissime ovatis obtusis laceratis ca. 1 mm. longis hyalinis brunneis. Pistilli ovarium globosum ca. 1 mm. diam. glabrum, ovulis 3; stylo ca. 2 mm. longo. Capsula globosa ca. 5 mm. diam. glabra.—PANAMA: COLON: Río Viejo, vicinity of Puerto Pilon, alt. 10 m., Feb. 2, 1947, *P. H. Allen 4099* (Herb. Missouri Bot. Gard., HOLOTYPE).

The fascicled inflorescences characterize this species, which resembles *Rourea glabra* superficially.

CARICACEAE

JACARATIA **dolichaula** (Donn. Sm.) Woodson, comb. nov.

Carica dolichaula Donn. Sm. in Bot. Gaz. 23:247. 1897.

This species exhibits the antesepalous corolla lobes, circumscissile calyx, caudate anthers, and laminately 5-lobed stigma of *Jacaratia*, as well as the palmately compound leaves.

LOGANICACEAE

SPIGELIA **aceifolia** Woodson, spec. nov. Fruticulus ca. 1 dm. altus e radice lignoso subtuberoso; ramis gracilibus teretibus inferne pauci-ramosis superne simplicibus dense minute pilosulis. Folia omnino opposita sessilia vel subsessilia trigonalia apice minute mucronata basi truncata vel obscurissime cordata 5–7 mm. longa basi 2.5–3.0 mm. lata coriacea margine valde revoluta supra glabra subtus minute pilosula. Flores in axillibus foliorum superiorum solitarii sessiles; calycis laciniis lineari-lanceolatis subsetosis 5 mm. longis glabris; corolla infundibuliformi rosea extus glabra, tubo proprio cylindraceo ca. 5 mm. longo, faucibus conicis ca. 3 mm. longis, ostio ca. 2.5 mm. diam., lobis oblongo-ovatis acutis ca. 5 mm. longis; staminibus in faucibus corollae inclusis, antheris ca. 1.5 mm. longis. Fructus ignotus.—BRAZIL: MINAS GERAIS: Serra do Cipó, Municipio Jaboticatubas, campo-margem est. rodagem, frequencia pouco, March 29, 1949, *M. Magalhaes 4,445* (Herb. Missouri Bot. Gard., HOLOTYPE).

Closely related to *S. stenophylla* Prog., which is glabrous and larger in all respects.

APOCYNACEAE

MANDEVILLA **ligustriflora** Woodson, spec. nov. Frutex volubilis; ramulis teretibus glabris maturitatem cortice rubro-brunneo striato atque lenticellato.

Folia opposita petiolata oblongo-elliptica subcaudato-acuminata basi obtusi 5–7 cm. longa 2.0–2.5 cm. lata coriacea omnino glabra supra nervo medio basi pauciglanduligero subtus pallidiora venis utrinque immersis nervo medio excepto; petiolis 0.5–1.0 cm. longis. Inflorescentia axillaris umbelliformis pauciflora; pedunculo ca. 1.5 cm. longo; bracteis lineari-lanceolatis minimis; pedicellis ca. 1 cm. longis; calycis laciniis ovatis obtusiusculis ca. 1.5 mm. longis scariaceis extus minute papillatis intus in margines pauciglanduligeris; corolla infundibuliformi pro genere parvissima extus rubro-tincta atque minute puberulo-papillata intus viridi, in alabastro rotundate ovoidea haud apiculata tubo proprio ca. 2 mm. longo basi ca. 1 mm. diam., faucibus tubulo-campanulatis ca. 3 mm. longis, ostio ca. 1.5 mm. diam., lobis ovatis ca. 1 mm. longis; antheris oblongo-sagittatis basi obtuse 2-lobatis dorso glabris; pistillo carpellis ovoideis glabris, nectariis 5 compresse oblongoideis ca. 1 mm. longis ovarium paulo superantibus; stigmate umbraculiformi ca. 2 mm. longo longe apiculato.—ECUADOR: Zamora-Huaico, ca. 6 km. s. e. of Loja, alt. 2300–2400 m., July 3, 1947, *R. Espinosa 1547* (Herb. Missouri Bot. Gard., HOLOTYPE).

This species approaches *M. jasminiflora* very closely indeed. The latter species, however, has narrower leaves with veins prominently elevated beneath and sunken above, and somewhat smaller corollas which are glabrous and conspicuously apiculate in the bud.

This occasion may be taken to confess that my description of *M. jasminiflora* (Woods. in Ann. Missouri Bot. Gard. 28:273. 1941) seriously errs in the description of the leaves as glandular the length of the midrib and of the calyx lobes as bearing a single opposite squamella, which together prompted me to place the species in the subgenus *Exothostemon* rather than in *Eumandevilla* where it actually belongs.

MANDEVILLA **Espinosae** Woodson, spec. nov. Frutex volubilis; ramulis crassiusculis dense ferrugineo-tomentulosis maturitate bene corticosis. Folia opposita brevissime petiolata late ovato-elliptica anguste acuminata basi cordata auriculis rotundatis convergentibus, 8–14 cm. longa 5–8 cm. lata membranacea supra sparsiuscule hirtella nervo medio basi pauciglanduligero subtus dense ferrugineo-tomentulosa; petiolo ca. 5 mm. longo. Inflorescentiae in axillas alternatas foliorum racemiformes pluriflores; pedunculis ca. 7–10 cm. longis dense ferrugineo-tomentulosis; bracteis minimis; pedicellis 1.0–1.25 cm. longis; calycis laciniis ovato-lanceolatis acuminatis 4–5 mm. longis extus ferrugineo-puberulis intus in margines pauciglanduligeris; corolla infundibuliformi viridi-gilva extus glabra; tubo proprio ca. 2 cm. longo basi ca. 1.5 mm. diam., faucibus late conicis ca. 7–8 mm. longis ostio ca. aequilato, lobis oblique obovatis ca. 3 cm. longis patulis; antheris oblongo-sagittatis basi minute emarginatis 8 mm. longis dorso glabris; pistillo carpellis oblongo-ovoideis ca. 2 mm. longis sparse minuteque pilosulis, cum nectariis 5 compresse ovoideis ca. dimidio aequantibus; stigmate umbraculiformi 3 mm. longo longiuscule atque anguste apiculato.—ECUADOR: Yacubiño (Zarumalado occidental de Chilchiles), alt. 2250 m., Sept. 3, 1947, *R. Espinosa 2077*

(Herb. Missouri Bot. Gard., HOLOTYPE).

Apparently most closely related to *M. glandulosa*, but differing conspicuously in the shallow, conical corolla throat.

MANDEVILLA **tricolor** Woodson, spec. nov. Frutex volubilis; ramulis parvis minute puberulis adultis crassiusculis cortice luteo-brunneo striato bene lenticellato. Folia opposita longiuscule petiolata oblongo-elliptica breviter acuminata basi late obtusa vel rotundata 2–4 cm. longa 0.8–1.5 cm. lata membranacea supra glabra nervo medio sparse puberulo excepto ibique basi pauciglanduligero subtus in axillas nervo medio inconspicue pilosula caeterumque glabra; petiolis 4–6 mm. longis minute puberulis. Inflorescentiae in axillas alternatas foliorum corymbiformes pluriflores; pedunculis ca. 1 cm. longis minute puberulis; bracteis 3–4 mm. longis subfoliaceis; pedicellis ca. 1.5 cm. longis minute puberulis; calycis laciniis oblongis vel oblongo-ellipticis acutis plus-minus inaequalibus 5–6 mm. longis foliaceis margine revolutis extus-intus sparse pilosulis intus cum squamellis ligularibus numerosis cinctis; corolla salverformi, tubo 1.0–1.2 cm. longo basi ca. 2 mm. diam. albo extus minute puberulo-papillato, lobis oblique obovatis ca. 6 mm. longis patentibus purpureis extus intusque puberulo-papillatis; antheris in tubi medio inserto anguste oblongis basi paulo concavis 4 mm. longis dorso glabris; pistillo carpellis obovoideo-oblongoideis glabris ca. 1 mm. longis squamellis 5 brevioribus; stigmate umbraculiformi ca. 2.5 mm. longo longe apiculato.—ECUADOR: Las Chinchas, 64 km. west of Loja, alt. 1700 m., March 1, 1947, *R. Espinosa 1332* (Herb. Missouri Bot. Gard., HOLOTYPE).

Apparently mostly closely related to *M. scutifolia*, and differing from it chiefly in the smaller leaves and very conspicuous, foliaceous calyx.

HOLALAFIA **Schumannii** (Stapf) Woodson, comb. nov.

Alafia Schumannii Stapf, in Fl. Trop. Afr. 4^1:197. 1904; Hutchinson & Dalziel, Fl. W. Trop. Afr. 2^1:45. 1931.

I have chanced upon the need for this new combination while identifying a few of Dr. J. T. Baldwin's plants of West Africa. An isotype of *Alafia Schumannii* (*Zenker 1662* in Herb. Missouri Bot. Gard.) shows not only the syncarpous ovary but the distinctive inflorescence structure of *Holalafia*. Incidentally, one of Dr. Baldwin's plants is a fruiting *Holalafia multiflora* Stapf: the follicles are linear, nearly 8 dm. long and about 1.5 cm. thick, and glabrous; the seeds have a body about 2.5 cm. long, the coma (with yellowish hairs about 6 cm. long) borne along a rostrum 1.5 cm. long, much as in *Funtumia*, but the hairs spreading and not retrorse (*Baldwin 13969* in Herb. Missouri Bot. Gard. and U. S. Dept. Agr.). I have never seen *Holalafia* and *Alafia* distinguished on the basis of seeds, but I suspect that in the former genus the coma may always be rostrate and in the latter sessile.

ASCLEPIADACEAE

MATELEA **Meyeri** Woodson, spec. nov. Frutex volubilis; ramulis gracilibus complicate pubescentibus (sparsiuscule eglandulo-pilosis cum trichomis brevioribus

plus minusve densioribus tum simplice eglandulosis tum brunneis bulbosis glandulosis interspersis). Folia opposita petiolata, lamina ovata cordata acuminata 8–9 cm. longa 4.5–5.0 cm. lata membranacea utrinque puberula (praecipue eglandulosa); petiolo ca. 3 cm. longo ut in ramulo vestito. Inflorescentia corymbiformis pluriflora; pedunculo ca. 1–2 cm. longo cum pedicellis ut in ramulo vestito; pedicellis gracilibus ca. 1.5 cm. longis; bracteis lineari-lanceolatis ca. 0.2 cm. longis. Flores ut creduntur gilvi extus plus minusve complicate pubescentes; calycis laciniis ovato-lanceolatis acuminatis ca. 0.3 cm. longis; corollae rotato-campanulatae tubo ca. 0.2 cm. longo basi ca. 0.1 cm. diam., faucibus ca. 0.2 cm. diam., lobis lineari-lanceolatis acuminatis erectis vel ascendentibus ca. 1 cm. longis; corona ample infundibuliformi carnosa corollae tubae valde adnata ostio ca. 3 mm. diam., sat integra sed obscure 5-loba quoque ligulam brevem gerente intus omnino carunculata; gynostegio brevi-stipitato ca. 1 mm. alto late 5-gono ca. 2 mm. diam., stigmate depresso, polliniis horizontalibus falciformi-subpyriformibus cum caudiculo breve ca. 0.5 mm. longis. Folliculi immaturi conspicue muricati dense complicate pubescentes.—MEXICO: TAMAULIPAS: open places along Río San Marcos, 5 mi. west of Ciudad Victoria, alt. 500 m., June 13, 1948, *F. G. Meyer & D. J. Rogers 2500* (Herb. Missouri Bot. Gard., HOLOTYPE).

A most curious species, obviously referable to my subgenus *Heliostemma* (cf. Ann. Missouri Bot. Gard. 28:221. 1941), but superficially very similar to *Matelea belizensis* (subgen. *Tiarastemma*).

MATELEA **Rogersii** Woodson, spec. nov. Frutex volubilis; ramulis gracilibus complicate pubescentibus (sparsiuscule eglandulo-pilosis cum trichomis brevioribus plus minusve densioribus tum simplice eglandulosis tum brunneis bulbosis glandulosis interspersis). Folia opposita longe petiolata, lamina late ovata cordata abrupte acuminata 15–20 cm. longa 13–15 cm. lata membranacea utrinque complicate puberula; petiolo ca. 6–7 cm. longo ut in ramulo vestito. Inflorescentia subumbelliformis pluriflora; pedunculo ca. 7–8 cm. longo cum pedicellis ut in ramulo vestito; pedicellis 2.5 cm. longis crassiusculis; bracteis anguste lanceolatis ca. 0.4 cm. longis. Flores virescentes; calycis laciniis elliptico-suborbicularibus obtusis subfoliaceis 0.7–0.8 cm. longis extus complicate pubescentibus; corolla late rotata eliganter reticulo-venosa extus intusque indistincte papillata ca. 2.5 cm. diam., lobis late ovato-deltoideis rotundatis minuteve mucronulatis ca. 0.8–1.0 cm. longis 1.3 cm. latis patulis; corona disciformi corollae faucibus adnata ca. 3 mm. diam., integra vel indistincte irregulariterque crenulata; gynostegio sessile ca. 1 mm. alto latissime 5-gono ca. 3 mm. diam., stigmate sat plano, polliniis horizontalibus subtriangulari-pyriformibus cum caudiculo late alato subaequilongo ca. 1 mm. longis. Fructus desunt.—MEXICO: NUEVO LEON: in arroyo, near Dulces Nombres, alt. 1400 m., Aug. 23, 1948, *F. G. Meyer & D. J. Rogers 3072* (Herb. Missouri Bot. Gard., HOLOTYPE).

A member of subgen. *Eumatelea* sect. *Reticulatae*, closely allied to *M. reticulata* and *M. Gentlei*, but differing from both in the much larger flowers, the large, suborbicular calyx lobes, and the nearly entire corona disc.

MATELEA **ionantha** Woodson, spec. nov. Frutices volubiles; ramulis gracillimis juventate minute pilosulis maturitate cortice sulcato dilute luteo tectis. Folia opposita longe petiolata, lamina ovata profunde cordata sensim acuminata 5–7 cm. longa 2.5–4 cm. lata membranacea utroque pagina sparsiuscule pilosula margine densius ciliolata, petiolo 2–2.5 cm. longo. Inflorescentia lateralis umbelliformis pauciflora, pedunculo 1–1.5 cm. longo, pedicellis ca. 5 mm. longis minute pilosulis cum glandulis minutissimis fuscis interspersis, bracteis minimis. Flores parvi purpurei, calycis laciniis ovato-lanceolatis acuminatis 4–5 mm. longis complicate pubescentibus, corolla rotato-subcampanulata extus intusque dense complicate pubescente ca. 1.5 cm. diam., lobis ovatis obtusis 5–6 mm. longis, patulis; corona annulata carnosa corollae faucibus valde adnata, segmentis 5 paene coalitis rhomboideis ca. 0.5 mm. altis 1 mm. latis planis dente truncato ca. 1 mm. alto excepto per saepto angusto ad gynostegio junctis. Gynostegium fere sessile ca. 2 mm. diam., stigmate depresso ca. 1.5 mm. diam. cum umbone lato, antherarum appendicibus apicalibus brevissimis, polliniis brevissime arcuatis fere quadratis ca. 0.3 mm. longis et latis margine superiore pellucido, caudiculis corpusculoque minimis.—MEXICO: VERA CRUZ: over shrubs at edge of oak forest near El Puerto, above Acultzingo, alt. 7600–7800 ft., Sept. 13, 1944, *A. J. Sharp 44,830* (Herb. Missouri Bot. Gard., HOLOTYPE).

Referable to subgen. *Heliostemma* (cf. Ann. Missouri Bot. Gard. 28:233. 1941), this species apparently is most closely allied to *M. cyclophylla* (Standl.) Woods., but differs in the vastly different foliage and smaller flowers with pollinia so short as to be scarcely arcuate.

MARSDENIA **Rotheana** Woodson, spec. nov. Sect. ELLIPTICARUM Rothe. Frutex volubilis; ramulis glaberrimis maturitate cortice singulare suberoso-fimbriatis. Folia modice petiolata, lamina ovato- vel oblongo-elliptica abrupte breviterque acuminata basi truncata vel plus-minus cordata 6–8 cm. longa 2.5–4.0 cm. lata firmiter membranacea glaberrima subtus pallidiora; petiolis 0.7–1.0 cm. longis sparse appresse pilosulis. Inflorescentia lateralis umbelliformis pauci- (plerumque 3-) flora; pedunculo ca. 0.5 cm. longo; pedicellis filiformibus 1.5–2.0 cm. longis glaberrimis; calycis laciniis ovatis obtusis vel rotundatis ca. 2 mm. longis minute ciliolatis intus cum squamellis minutis alternatis 1–2; corolla campanulato-rotata extus intusque glaberrima lutea, tubo ca. 2.5 mm. alto faucibus ca. 6 mm. diam., lobis late ovato-trigonalibus late acutis ca. 6 mm. longis patulis. Gynostegium dimidio exsertum ca. 4 mm. longum; stigmate late conico; coronae squamis duplicibus dorso subquadratis ca. 2 mm. longis et latis processu aciculari paulo breviori. Fructus ignoti.—PANAMA: COCLÉ: Cerro Pajita, region north of El Valle de Antón, alt. 3500 ft., May 12, 1947, *P. H. Allen 4495* (Herb. Missouri Bot. Gard., HOLOTYPE).

This is the first species of Rothe's section ELLIPTICAE (cf. Engl. Jahrb. 52:424. 1915) to be described from the continent. Its closest relative would appear to be *M. Dussii* Schltr. of Martinique, which has smaller, reddish flowers with much shorter pedicels.

SOME AMERICAN CARBONIFEROUS FERN FRUCTIFICATIONS[1]

SERGIUS HARRY MAMAY[2]

Introduction

Prior to the discovery of coal balls and the development of techniques which made possible the cutting of petrifactions for detailed anatomical studies, the attention of paleobotanists was mostly limited to considerations of impressions and compressions. The resultant early studies demonstrated that certain plants which bore fern-like foliage, often preserved in exquisite fashion, constituted conspicuous elements in the Coal Age floras of Europe and America. To Adolph Brongniart falls the bulk of the credit in the nomenclature of these foliar compressions.

At an early date fertile specimens bearing circular groups of sporangia upon the lower surfaces were found among the fern-like leaf impressions. Such specimens, the majority of which were referable to the genus *Pecopteris*, were, by virtue of what information could be gathered from the compressed fructifications, commonly regarded as constituting a marattiaceous element in the Coal Age floras. This opinion met with little controversy until the early part of the 20th century, when it was demonstrated that at least some of the Carboniferous plants to which fern-like foliage was attributed bore seeds. This initiated our knowledge of the pteridosperms, an extremely interesting group which has since been much investigated. While some authors preferred to look with doubt upon the marattiaceous affinity of the pecopterid fructifications, the striking anatomical similarity of the fossil stem *Psaronius* to the living marattiaceous genus *Angiopteris*, along with other factors, appeared to strengthen the validity of the Carboniferous Marattiaceae, despite the supposed likenesses between the pecopterid fructifications and certain of the pteridospermous microsporangiate fructifications.[3]

Anatomical studies of coal ball plants, begun in England in 1868 by Binney and further pursued by such outstanding anatomists as Williamson and Scott, demonstrated the presence of an additional complex in the Carboniferous floras, the primitive ferns or Coenopterideae (Seward, 1910). Although these plants are yet incompletely known, the nature of their vascular systems and fructifications indicates affinities with certain of the ferns rather than with other vascular cryptogams.

In spite of the fact that investigations of coal balls in America have been under way for only two decades, we have achieved at least an introductory picture of our Coal Age floras. Numerous coal ball localities have been discovered in Illinois, Iowa, Indiana, and Kansas, with the result that significant literature has accumu-

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[1] An investigation carried out in the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor in Philosophy at Washington University. This study was aided by a grant from the Penrose Fund of the American Philosophical Society.

[2] John Simon Guggenheim Fellow, University of Cambridge, England, 1950-51.

[3] This problem is considered in greater detail in the summary.

lated.[4] It is known that American Carboniferous floras contained liberal representatives of the Marattiaceae, Pteridospermae, and Coenopterideae, and while considerable attention has been directed toward studies of the anatomy and fructifications of the American pteridosperms, much remains to be learned about the Marattiaceae and Coenopterideae, chiefly from the standpoint of their fructifications. A few brief descriptions of the vegetative organs and fructifications of these plants have been published, yet their abundance in recent collections indicates that this represents only a beginning toward a comprehensive knowledge of these elements of the American floras.

The scarcity of literature dealing with petrified fructifications might be explained thus: The organs in question are extremely small and rarely occur in sufficient quantities to constitute conspicuous masses. The better-known descriptions have been based chiefly on remarkably large aggregations of fructifications such as *Botryopteris forensis* Renault and *B. globosa* Darrah. Such specimens are rare. To undertake a study of these organs involves painstaking systematic inspections of many petrifactions under reasonably high magnification, a process which might easily be deferred in favor of investigation of larger, more conspicuous stems, seeds, etc.

The present paper treats the various fructification species present in coal balls from various American localities. These have been critically compared with descriptions of all related species from both Europe and America, with the result that several distinctly new entities are recognized. These include three new species of *Botryopteris* Renault; one new species of *Cyatheotrachus* Watson, the generic concept of which is emended; three new species of *Scolecopteris* Zenker, and a new variety of *S. minor* Hoskins, in addition to an emendation of and supplementary data concerning *S. latifolia* Graham; and a new genus, *Eoangiopteris*, which is postulated as a progenitor of the *Angiopteris* type of modern marattiaceous sori.

In recognizing new species, the size of sporangia, structure of sporangial walls, and the number of sporangia in the fructifications are carefully considered as criteria, with critical attention given to the range of variation which might be expected within the limitations of a species. Where possible, details of the supporting pinnules are also noted. All these features appear to be trustworthy criteria for speciation, but it has been found that the spores present the single outstandingly dependable basis for comparison. While variation among the spores of the various species of a given genus is extreme, from the standpoints of both size and morphology (the spores of *Scolecopteris*, for instance, range from 10 to 80 μ in diameter, and may be of either bilateral or tetrahedral symmetry), they are remarkably constant among different specimens of a given species[5]; considering the spores together with the other variables mentioned above, a reliable concept of the species complex of a fructification genus may be arrived at.

[4] A comprehensive review of American coal ball literature, is being prepared by H. N. Andrews, for a future number of the 'Botanical Review.'

[5] In limiting the diagnostic value of these spores to the specific level we concur with Knox (1938) who wrote: ". . . and even for genera there are not many examples where spore characters could be held to be diagnostic."

The accepted practice of designating holotypes in describing new species of fossil plants is hardly practicable when dealing with fructifications as small as those involved in this study. With a stem specimen of a centimeter or so in diameter and several centimeters in length, it is possible to make sufficient sections to gain a thorough understanding of the specimen and still preserve enough material to constitute a holotype for future reference. However, the fructifications described in this paper scarcely exceed a single millimeter in length, making it impossible to arrive at a reconstruction from a single specimen. Fortunately, their smallness is generally compensated for by their abundance in the coal balls. In several cases, the initial cut of a coal ball has exposed numerous fructifications sectioned in all planes and levels. Thus we have been able to obtain a complete and accurate concept of the nature of a fructification species by examination of a single peel. In more critical studies of exceptional specimens, however, serial peel sections were employed. Since the descriptions of new species are based upon not one but several specimens, we will cite *syntypic* slides which have been made from peels selected because of their abundant fructification content or excellence of preservation, or both.

Materials and Techniques

At the beginning of this investigation, attention was concentrated on a collection of coal ball slabs from the Urbandale Mine near Des Moines, Iowa, particularly rich in fern fructifications, and it was in them that the majority of the specimens described were found. This material was generously donated to the Washington University collection by Mr. Frederick O. Thompson of Des Moines, whose collecting activities during the past several years have indeed proven a boon to recent American paleobotanists.

As the investigation proceeded, coal balls from various other localities were collected and inspected. Those which have produced fructification material are:

1. The Urbandale Mine, located 1.2 miles west of Des Moines, Iowa, on U. S. Highway #6 (Walnut Township, Dallas County). This coal lies in the Des Moines Series of the Pennsylvanian. (See Andrews and Kernen, 1946.)

2. Berryville, Illinois. This small outcrop, which is found in a stream bed approximately 2 miles northeast of Berryville, Illinois (Sumner Quadrangle, Lawrence County), lies in the upper portion of the McLeansboro Group of the Pennsylvanian of Illinois.

3. Big Creek #1 Mine of the Wasson Coal Mining Corporation, which is located approximately 2 miles south and 1.5 miles east of Lynnville, Indiana. This coal (Petersburg V) lies in the upper portion of the Des Moines Series.

4. Strip pits of the Pittsburgh and Midway Coal Company, located 4 miles south of Mineral, Kansas (Columbus Quadrangle, Cherokee County). This coal is known as the Fleming Coal, and lies in the upper one-third of the Cherokee Shale, which is found in the Des Moines Series of the Pennsylvanian.

5. Shore, Lancashire, England. The material from this locality consists of a single small coal ball fragment. This coal seam lies in the Great Coal Ball Horizon of the Lanarkian Series. (See Schopf, 1941.)

While each of these localities has produced fern fructifications in some abundance, none has approached the Urbandale for the number of species present. However, at the time of this writing, the Mineral, Kansas, material is only beginning to be investigated, but it promises to equal or even surpass the Urbandale locality in diversity of the flora.

The peel technique followed is essentially that outlined by Pannell (1942). In a few instances it was necessary to make successive peels at intervals as close as possible, due to the smallness of the specimens. Those specimens selected for illustrative purposes were cut from the peel, mounted in Clarite on glass slides, and photographed with Panatomic X sheet film and a green Wratten filter.

All the slides cited are catalogued in the Washington University paleobotanical collection.

COENOPTERIDALES

While much is known of the vegetative anatomy of the coenopterids, or primitive ferns, relatively little is known of their fructifications. The various genera are easily distinguished on the basis of their petioles, which exhibit great diversity of structure, in contrast to the generally simple and uniform organization of the stems. Although considered to be an extremely primitive group of vascular plants, they nevertheless embrace genera with certain structural modifications suggestive of higher groups, e. g., the axillary branching of *Ankyropteris*, the weak but distinct secondary thickening in the stem of *Botrychioxylon*, and the compact, synangial fructifications of *Chorionopteris*, which were borne on well-developed laminae.

Regarding the fructifications, the diversity of structure within the coenopterids is great. In the most primitive representative, *Stauropteris*, the sporangia are solitary, exannulate, massive-walled, and borne terminally on the ultimate ramifications of the radially symmetrical "frond." Between this extreme and that seen in *Chorionopteris*, various intermediate forms are known (this series is considered more critically in the conclusion of this paper). The extremely diverse structure of the petioles, the axillary branching, and the cambial activity, prompt the conclusion that the coenopterid ferns must have constituted an extremely plastic evolutionary plexus from which several lines of fern (and probably pteridosperm) development began to emerge early in the history of vascular plants. The appearance in the late Paleozoic of fern fructifications which show strong affinities with the Schizaeaceae *(Senftenbergia)*, Gleicheniaceae *(Oligocarpia)*, and Marattiaceae *(Scolecopteris, Cyathotrachus*, etc.*)*, along with stem remains whose anatomy indicates osmundaceous affinity *(Thamnopteris, Zalesskya)*, appears to strengthen such a supposition. This would also seem to imply an extremely early differentiation of both the eu- and leptosporangiate development of fructifications, very

likely much earlier than the development of laminate foliar organs.

The vegetative remains of several coenopterid genera have been reported in American paleobotanical literature.[6] Stems and petioles of *Ankyropteris, Botryopteris, Etapteris, Stauropteris, Anachoropteris,* and *Grammatopteris*[7] have been reported in America. However, only the genus *Botryopteris* is known from its fructifications, these having been reported by Darrah (1939) and Graham (1935). Graham also described a new fructification genus of apparently coenopterid affinity, but which has not been correlated with any stem genus *(Notoschizaea robusta)*. He pointed out a strong resemblance of *Notoschizaea* to the fructification *Corynepteris,* however.

The coenopterid fructifications found during this investigation are representatives of the genus *Botryopteris* Renault, the vegetative organs of which are found in some abundance in American coal balls. The history of the fructification species of *Botryopteris* follows:

BOTRYOPTERIS Renault, Ann. Sci. Nat. (Bot.) VI, 1:223–229. 1875.

Renault's type species, *B. forensis,* was based upon silicifications from the Permo-Carboniferous of Autun and St. Etienne. Renault was fortunate in finding both the vegetative organs and the fructifications, with no reason for doubt as to the correlation between the two. The sporangia were produced in small clusters on the termini of the ultimate ramifications of a much-branched "frond," resulting in a large compound fructification containing possibly several thousands of sporangia. The individual sporangia are shortly pedicellate, more or less pyriform, and attain lengths of 2 mm. and diameters of 1 mm. The sporangial walls are, according to Renault, ". . . . formées d'un seul rang de cellules polyédriques . . .", and are distinctive in possessing a multiseriate annulus-like band of enlarged cells which extends from the apex to the base along one side of the sporangium. Dehiscence occurred by a longitudinal cleft along the thin opposite wall. The spores are spherical, apparently smooth-walled, and attain diameters of 70 μ.

In the same publication Renault described a second species of *Botryopteris (B. dubius)* which he later transferred to the genus *Zygopteris.*

Scott (1910) described a group of sporangia from the Lower Carboniferous of Pettycur, which was found in intimate association with a petiole of *B. antiqua.* The sporangia measure from 240 to 280 μ in diameter, with the cells of the annulus reaching 60 μ in diameter. The spores average 25 μ in diameter, and are somewhat triangularly flattened. A structure which he interpreted as of possible indusial nature was found associated with the sporangia. Scott (1920) has also reported similar small botryopterid sporangia in association with the Lower Carboniferous species *B. hirsuta* and *B. ramosa.*

Graham (1935) described botryopterid petioles and sporangia from the Upper Pennsylvanian of Illinois, naming them *B. americana.* Among the fructifications

[6] Darrah (1941) has summarized the American coenopterids.

[7] An excellent specimen of *Grammatopteris* has only recently been found by us in a coal ball from Berryville, Illinois. This is apparently the first known occurrence of this genus in this country.

he noted "sterile" sporangia which he termed "specialized" without further elaboration. Dimensions are not cited, but judging from the size of the drawings and the magnifications given the sporangia appear to be approximately .70 mm. wide and 1.30 mm. long, with spores about 30 μ in diameter.

The second American species, *B. globosa* Darrah (1939), is from the Upper Pennsylvanian of Iowa. This remarkable fructification is the American counterpart of Renault's *B. forensis*, consisting of innumerable sporangia borne in terminal tufts on a highly branched "frond."

During the present investigation *Botryopteris* fructifications have been found in coal balls from the Urbandale Mine, Iowa, and Berryville, Illinois. These are much smaller than previously described species, with the exception of those reported by Scott. Although they do not differ greatly among themselves in sporangial dimensions, three distinct species are recognized, based chiefly on spore morphology.

BOTRYOPTERIS **fecunda**, sp. nov. (figs. 1–4).

Numerous clusters of small sporangia are present in coal balls # 437A, 442, 679, and 680, from the Urbandale mine. Their compact aggregation in all cases suggests that these clusters represent small portions of highly compound fructifications comparable in complexity to those of *B. forensis* and *B. globosa* (fig. 3). It is apparent that each cluster consists of from 5 to 20 sporangia, terminating small frond ramifications. The attachment to these ultimate branchlets has only been noted in a few isolated cases, the branchlets themselves being very poorly preserved.

The individual sporangia are shortly pedicellate, and ovoid-ellipsoid in longitudinal section (fig. 1); in transverse section perfectly oval (fig. 2). The sporangia reach a maximum of .45 mm. in length and .25 mm. in diameter.

The sporangial walls are but a single cell thick. As seen in transverse section, the wall displays a differential thickening which served as an annulus. The largest cells of the annulus are approximately 50 $\times$ 50 μ in their transverse dimensions and about 75 μ in length. Their inner and radial walls are thicker than the free outer walls. The size of the cells decreases gradually, with the smallest cells measuring only 8–10 μ in thickness. Dehiscence occurred by means of a longitudinal cleft along the thinnest portion of the wall. The differential thickening of the sporangial wall may be clearly seen in figs. 1 and 2.

Numerous well-preserved spores are present in nearly every sporangium. They are of radial- trilete morphology (see fig. 4). The commissural, or inner surfaces, of the spores are compressed into three nearly equilateral triangular surfaces, each measuring about 36 μ along its basal side. The inner sides are delimited by a prominent triradiate ridge which extends nearly to the corners of the inner face. The spore walls are finely reticulate, the differential thickening producing extremely thin and translucent spots between the thickened ridges.

The small size of the sporangia and the distinctness of the spores warrant recognition of this fructification as a new species. The specific name *fecunda* is

proposed in reference to the prolificity with which the sporangia were produced.

Specific Diagnosis: Sporangia borne in compact terminal clusters of 5 to 20 each, pedicellate, ovoid-ellipsoid, reaching .45 mm. in length and .25 mm. in width. Largest cells of annulus averaging 50 × 50 μ in transverse dimensions. Spores radial, trilete, averaging 36 μ along the base of each triangular commissural surface, and with pronounced triradiate ridges; spore walls finely reticulate, with thin, translucent areolae.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1676–1680.

BOTRYOPTERIS **spinosa**, sp. nov. (figs. 5–8).

A single group of rather loosely aggregated sporangia with dimensions similar to those of *B. fecunda*, but of slightly different shape and with entirely distinct spores, was found in WCB 437B, from the Urbandale mine (fig. 6). The sporangia are much more loosely arranged than those of *B. fecunda*. The pedicellate attachment to a small ultimate rachis was clearly observed in one case (fig. 7). The sporangia average .50 mm. in length and .25 mm. in diameter. In longitudinal section they are somewhat narrowed at the base, resulting in a pyriform aspect. The sporangial walls are a single cell thick. The largest cells of the annulus measure approximately 50 × 50 μ in transverse dimensions and 70 μ in length (fig. 8).

The spores (fig. 5) are perfectly spherical, averaging 45 μ in diameter. A faint triradiate ridge is present, each leg not exceeding 10 μ in length. The spore walls are smooth, but distinct in being sparsely studded with blunt spines reaching 6 μ in length and averaging 2 μ in diameter. Calculations indicate a comparatively low spore output, not exceeding a hundred spores per sporangium.

This species is named *spinosa* with reference to the spinose ornamentation of the spore walls.

Specific Diagnosis: Sporangia borne in loosely aggregated clusters terminating the ultimate ramifications, shortly pedicellate, pyriform, averaging .50 mm. in length and .25 mm. in diameter. Largest cells of annulus averaging 50 × 50 μ in transverse dimensions. Spores spherical, trilete, averaging 45 μ in diameter, with faint triradiate ridges; spore walls sparsely provided with blunt spines reaching 6 μ in length and 2 μ in diameter.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1681–1683.

BOTRYOPTERIS **illinoensis**, sp. nov. (figs. 9, 10).

This description is based upon numerous isolated sporangia and one small cluster of eight, found in WCB 714 and 715, from Berryville, Illinois.

The sporangia are nearly spherical (fig. 10). The sporangial walls are a single cell thick, with the largest cells of the annulus measuring approximately 70 μ radially and 40 μ tangentially. No evidence of a sporangial pedicel has been observed.

The spores are quite distinctive (fig. 9). They are radial and trilete, with axial dimensions much smaller than the transverse. This is not due to crushing, however, as the spore walls are always fully distended. As seen in the transverse plane, the spores are roughly triangular, with rounded corners and markedly concave sides. The distance between corners averages 23 μ; the distance between one corner and the opposite concavity in the spore wall averaging 18 μ. The rounded tips average 10 μ in width. In axial dimensions the spores average 10 μ. The walls are thin, with a faint triradiate ridge, the legs of which extend approximately two-thirds of the distance to the tips of the lobes. Otherwise there are no distinct markings on the walls.

Although this fructification is entirely distinct from all other American fructification species of *Botryopteris,* it corresponds quite closely to those reported by Scott (1910) in association with the English species *B. antiqua, B. hirsuta,* and *B. ramosa.* However, the absence of these species in American coal balls and their greater geological age make it seem quite unlikely that the fructifications are conspecific with the Illinois specimens. Furthermore, the Berryville locality has produced to date two stem species of *Botryopteris,*[8] either of which may ultimately prove to have borne these sporangia. For this reason, in addition to the contrasting characters found between the Illinois specimens and all other American species, this fructification is recognized as an additional new species, the name *illinoensis* being proposed in recognition of its place of origin.

Specific Diagnosis: Sporangia ovoid, averaging .40 mm. in length and .30 mm. in diameter. Largest cells of the annulus averaging 70 $\times$ 40 μ in transverse dimensions. Spores radial, trilete, axially flattened, with rounded corners and concave sides, 10 μ in axial dimensions and 23 μ between corners; spore walls smooth, with faint triradiate ridges.

Age: McLeansboro Group of the Pennsylvanian.

Locality: Berryville, Illinois.

Type Slides: #1684–1686.

A comparison of the various species is presented in tabular form on the following page.

DISCUSSION

The sporangia discussed in the preceding pages, while belonging to an archaic fern genus, are striking in several respects. They have very delicate sporangial walls, a single cell thick. There is a differential thickening of the wall, suggestive of a primitive annulus. The sporangia themselves are very small, comparing closely with living osmundaceous sporangia in size. Finally, in at least the one species *Botryopteris spinosa,* spore output is relatively low, closely comparing to the Osmundaceae in this respect also.

While the coenopterid ferns have been variously known as the Primofilices (Arber, 1906), Coenopterideae (Seward, 1910), and Inversicatenales (P. Bertrand,

[8] In a recent communication, Dr. W. N. Stewart, of the University of Illinois, reported having found specimens of *B. radiata* Darrah in Berryville material. This locality is also the source of a yet unpublished new species of *Botryopteris.*

1909), they have invariably been considered as *eusporangiate* forms. As defined by Goebel (1880), one of the implications of this term is a sporangial jacket more than one cell thick. In this consideration alone the sporangia of *Botryopteris* fail to conform to the eusporangiates. While it is true that the bulky walls of sporangia of *Etapteris*, *Chorionopteris*, and *Stauropteris* allow no alternative but to consider the genera to be of eusporangiate nature, the thin-walled sporangia of *Botryopteris*, pointed out by Renault in his original description of the fructifications and by Scott and Bower, seem to offer grounds for doubting the validity of such an arbitrary scheme of classification.

COMPARISON OF THE VARIOUS FRUCTIFICATION SPECIES OF *BOTRYOPTERIS*

Species	Sporangial dimensions	Spore size	Spore morphology	Spore ornamentation
B. forensis Renault	1 × 2 mm.	70 μ	Spherical, trilete	Apparently smooth
B. americana Graham	1.30 × .70 mm. (?)	30 μ (?)	?	?
B. globosa Darrah	1.50 × 1 mm.	50–65 μ	Spherical, trilete	Smooth
B. sp. Scott	.28–.24 mm. diameter	25 μ	Triangularly flattened	?
B. fecunda Mamay	.45 × .25 mm.	36 μ along one side	Tetrahedrally compressed	Finely reticulate
B. spinosa Mamay	.50 × .25 mm.	45 μ	Spherical, trilete	With blunt spines
B. illinoensis Mamay	.40 × .30 mm.	23 μ between lobes	Axially flattened, triangular, with concave sides	Smooth

Hirmer (1927), although adhering rigidly to the eusporangiate concept of the coenopterids, has taken a forward step in introducing a scheme of fern classification in which the Osmundaceae are placed in a position intermediate between the Leptosporangiatae and Eusporangiatae, the subdivision to which they are assigned (Protoleptosporangiatae) enjoying equal rank with the Eu- and Leptosporangiatae. The genus *Botryopteris* cannot be conclusively assigned to either of these two main groups, in view of the admixture of both primitive and advanced characters. It is highly probable that as our knowledge of the fossil ferns advances, the coenopterids eventually will be considered to be less closely interrelated than they have been previously, and that the great structural differences to be found among their fructifications will gain recognition in a revised classification.

Marattiales

This order, embracing a single family with seven living genera and a large complex of extinct forms, is characterized by its eusporangiate, exannulate fructifications consisting of more or less synangial, clearly circumscribed sori which are borne superficially.

The majority of the Carboniferous Marattiaceae bore radially symmetrical sori, and as has been pointed out previously by Hoskins (1926) and Graham (1934), these fructification genera were placed by Stur (1883) in a suborder of the Marattiales, the Asterotheceae. This suborder includes only fossil forms, now totaling six genera, two of which (*Scolecopteris* Zenker and *Cyathotrachus* Watson) have been found to occur rather abundantly in the American coal balls investigated in this study. In addition to these two genera, whose histories are reviewed in succeeding pages, the Asterotheceae include the following:

Acitheca Schimper: Synangia sessile; sporangia attached at their bases to a central column, with distal portions free; sporangial apices long and bristle-like. (For historical details see discussion of *Scolecopteris*.)

Asterotheca Presl: Synangia sessile; sporangia attached to a central receptacle, but free distally, their long axes parallel to the plane of the pinnule. Genus founded by Presl (Corda, 1845), and originally considered to be gleicheniaceous by Corda. Several species known, chiefly from compression material.

Ptychocarpus Weiss: Synangia pedicellate; sporangia enclosed in a continuous synangial sheath, and fused to a central column extending through the entire length of the synangium. Genus founded in 1869; the best-known description is that of *P. unita* Brongniart, by Renault (1896). (See fig. 11.)

Sturiella Weiss: Synangia pedicellate; sporangia basally fused but free above, each sporangium with an apical annulus-like structure. Genus founded by Weiss (Zeiller, 1890); a detailed description presented by Renault (1883) as *Pecopteris intermedia*. The presence of the annulus-like structure, along with the synangial nature of the fructification, has caused *Sturiella* to be regarded as intermediate between the Marattiaceae and Osmundaceae.

These genera are limited mainly to strata of Upper Carboniferous age, and are all known to exist in organic connection or intimate association with foliage of the *Pecopteris* type.

Although many of the petrifications investigated in this study contain an abundance of fructifications belonging to several genera, *Asterotheca* and *Ptychocarpus* are totally lacking. While petrified specimens of these two genera have been reported in the literature, they are represented in large part by compressed specimens. This situation suggests a problem in preservation phenomena.

It has been pointed out by Kidston (1925) and Arnold (1947) that the single major difference between *Scolecopteris* and *Asterotheca* lies in the fact that the former is pedicellate, the latter sessile. In all other features, such as size and shape of the sporangia and manner of dehiscence, they are essentially alike. Studies of petrified *Scolecopteris* specimens have shown that with maturity the sporangia be-

came radially extended from each other, much as the ribs of an opening umbrella; in this condition they closely approach the typical aspect of *Asterotheca*, discounting their pedicellate nature. If sufficiently extended prior to compression, the fructifications would eventually be preserved with the sporangia arranged in a typical asterothecoid fashion, with the pedicel totally obscured from view. There would thus be no dependable method of determining the true generic affinity of the specimen. Although it is not my intent to question the validity of the genus *Asterotheca*, the following pertinent facts should be given careful consideration:

1. Petrified fructifications referable to *Asterotheca* have not been recognized during this study,[9] while *Scolecopteris* has been found in great abundance.

2. While the vast majority of accounts dealing with *Asterotheca* have been based on compression material, the exact reverse holds true for *Scolecopteris*.

Due to the reasons presented above it would appear that positive identification of compressed fructifications must not be made without careful consideration of the possibilities for generic confusion. A similar situation might exist in the genera *Ptychocarpus* and *Cyathotrachus*, which differ only in the extent of the central column, a feature which does not readily lend itself to accurate determination in the compressed form. While *Ptychocarpus* is found prolifically as compressions, in only two instances has it been reported in the petrified state in American literature.[10] On the other hand, while three species of *Cyathotrachus* are known from petrifactions, not a single compressed specimen has ever been reported, all compressed fructifications in which the sporangia are surrounded by a continuous synangial sheath being referred to *Ptychocarpus*.

CYATHOTRACHUS Watson, emend. Mamay.

C. ALTUS Watson, Roy. Micr. Soc. Jour. 1906. 1–3.

C. BULBACEUS Graham, Bot. Gaz. 95:459–461. 1934.

The genus *Cyathotrachus* is the most recent addition to Stur's (1883) Asterotheceae. Although the publication in which the genus was established appeared several years later than that of Stur, Graham (1934) was the first to recognize the asterotheceous affinity of the fructification and point out the necessity for including it within that group.

Watson's type species, *C. altus*, is from the Lower Coal Measures of England. His discovery of a cup-like tracheidal structure in the base of the synangium led to the adoption of the generic name *Cyathotrachus*. The specific name *altus* refers to the height of the fructification. Although his description does not include a clear statement of the generic characters, he apparently considered the tracheidal cup to be of primary importance. This concept has, however, been altered by subsequent discoveries. Graham, in describing the second species, *C. bulbaceus*, from the Upper Pennsylvanian of Illinois, failed to recognize any such structure

[9] Benninghoff (1943) briefly mentioned the presence of *Asterotheca* in Indiana coal balls.
[10] *Ptychocarpus* has been reported by Benninghoff (1943) and Hoskins (1933).

in his specimens and considered that its presence or absence could possibly constitute a generic difference. I have studied several scores of specimens from Iowa coal balls, paying particular attention to this detail, and I did not observe the tracheidal cup in a single fructification. Notwithstanding, there is ample evidence to support the belief that the two above-mentioned species and a third, described below, are congeneric. It appears that the fructification was inaptly named, since the generic name refers to an inconstant character which should be considered to be of only specific importance. The character of prime generic importance would seem to be the cup-like arrangement of the fructification itself.

An emended concept of the genus is presented in the following diagnosis:

Generic Diagnosis: Synangia pedicellate, circular, containing several more or less elongate, exannulate sporangia, the entire fructification enclosed in a continuous outer synangial sheath, with the exception of the apical pore. Basal portion of the synangium with a central column; apical portion hollow and cup-like.

CYATHOTRACHUS **altissimus**, sp. nov. (figs. 12–16).

The description is based upon numerous specimens scattered through several of the Urbandale coal ball slabs from the Thompson collection. Although usually occurring singly, a few specimens consisting of several closely associated synangia were found. In several instances it was possible to select specimens for further study with the naked eye, because of the large size of the fructifications and the characteristic bright golden color of their spore masses, which were in striking contrast with the less conspicuously colored matrix.

Although the number of sporangia in a synangium ranges from 5 to 9, those with 7 are predominant. The innermost walls of the sporangia are fused with the tissue of a central column[11] that extends slightly beyond the middle of the synangium. The column flares out somewhat at the distal end, forming a shallow saucer-like structure beyond which the synangium is hollow and resembles a deep cup. Proximally, the column extends beyond the bases of the sporangia to form the short synangial pedicel. The column is composed of elongate thin-walled cells averaging approximately 25 μ in diameter and 300 μ in length. There is no evidence of vascular elements in this structure.[12] Average dimensions of the central column are approximately .20 by .80 mm. (fig. 12).

Individual sporangia average 1.50–1.80 mm. in length and .20–.45 mm. in diameter, the radial dimensions being slightly greater than the tangential, due to lateral appression with adjacent sporangia. The synangia as a whole average .80–.90 mm. in diameter. Throughout the portion of the synangium that is traversed by the central column, the lateral walls of the sporangia are so closely appressed as to present the appearance of a single wall (fig. 15), but progressing distally beyond the termination of the column the walls of adjacent sporangia can

[11] Watson (1906) termed this structure a "columella", but this usage is questionable, since the column is not, in this case, a structural entity of the sporangium proper.

[12] Watson (1906) found tracheids in this column, and Graham (1934) termed this tissue "transfusion tissue" without further elaboration.

be distinguished from each other. The character of the sporangial walls is best seen in dehiscent synangia (fig. 16). The cells are thin-walled, and there appears to be only one layer. The outer surface of the synangium is enclosed by a continuous layer of thin-walled cells corresponding very closely to the synangial wall found in *Ptychocarpus*. This layer of tissue partially fills the angles created where the lateral walls of adjacent sporangia depart from each other, and varies from one to three or four cells in thickness. Serial sections indicate that the synangial wall increases in thickness as the distal end of the synangium is approached. This structure is shown in fig. 13. The fact that it is not present in all specimens indicates that it may have been rather fragile tissue, probably drying at maturity and being either blown off by the wind or rubbed off by friction with adjacent synangia.

The cellular details of the pinnules were observed in a few isolated fragments. The upper epidermis is highly cuticularized and shows no cellular detail, being seen only as a dense black line. Beneath the palisade layer the cells are rather loosely aggregated and show no apparent differentiation, with the exception of the one or two lowermost layers of cells, which are flattened in the plane of the lamina surface. These appear to be a continuation of the pedicel, showing a close similarity to its tissue both in size and shape of cells. The pedicel is very short and thick, and the tissues composing it are not distinguishable from those of the central column. The manner in which the synangia were oriented upon the surface of the lamina was observed in one specimen. This consists of several distinct rows of compactly arranged synangia oriented at right angles to a structure which appears to be the midrib of a penultimate pinnule, two adjacent rows of synangia probably representing the fructifications produced by a single ultimate pinnule. Unfortunately, that portion of the coal ball containing the remainder of the specimen was not among the slabs presented by Mr. Thompson, and we have not been able to ascertain the relationship between the rows of synangia and the parent pinnules, or the nature of the pinnules. Since the two previous species are known to be in close association with *Pecopteris* foliage, and since the orientation of the synangia in this specimen seems to correspond closely with that of other asterotheceous pecopterid fructifications, it seems safe to assume that this species was borne on foliage of the *Pecopteris* type.

Neither Watson nor Graham described the dehiscence of *Cyathotrachus*, but fortunately many of the Iowa specimens illustrate that feature very well. Dehiscence was accomplished by means of longitudinal slits along the inner walls of the sporangia, extending from the sporangial apices as far as the proximal limits of the hollow portion of the synangium. Although no specialized stomial or annulate structures were present, the inner surfaces of the sporangia, being the thinnest, offered the line of least resistance, with the results described here. Dehiscence of the sporangia was accomplished by a rupturing of the outer envelope of the synangium and separation of the closely appressed walls of adjacent sporangia; this release of both lateral and peripheral tension allowed the sporangia to

assume a more nearly cylindrical appearance than that displayed prior to dehiscence. That portion of the sporangium adjacent to the central column, however, was not altered by dehiscence; lateral walls remained closely appressed with those of the adjacent sporangia, and the synangial wall remained intact. Figure 15 shows a transverse section of a sporangium that has already shed its spores. Here the section has been taken through the central column, and the synangial wall is still a continuous tissue surrounding the entire structure. Dehiscence is further illustrated in fig. 16, in which the spores are being shed into the hollow synangial cup.

Spores of this species are small, with bilateral-monolete symmetry, averaging 12 × 20 μ in dimensions. The walls are smooth, with the exception of a single faint longitudinal suture that is seen on the concave side of better-preserved spores. Judging from the relative dimensions of the spores and sporangial cavities, it appears that several thousands of spores were produced in each sporangium. Figures 13 and 14 illustrate the bean-like shape of the spores and the abundance in which they were produced. Tetrads have not been observed.

Cyathotrachus altissimus differs in several ways from the two previously described species. In general proportions it corresponds rather closely with the type species, *C. altus*, but differs sufficiently in size, number of sporangia, and spore characters to warrant recognition as a separate species; likewise the differences from *C. bulbaceus* are equally significant. The more important characters of the three species are presented in the following table:

	C. altus Watson	*C. bulbaceus* Graham	*C. altissimus* Mamay
Sporangial dimensions	.20 × .70 mm.	.30–.35 × .65 mm.	.20–.45 × 1.50–1.80 mm.
Number of sporangia per synangium	4–7	4–6	5–9
Spores	Ovoid, 12.5 × 15 μ	Round, 18 μ in diameter	Bilateral, 12 × 20 μ

In reference to the proportionately greater height of the synangium than that of the type species, the specific name *altissimus* is proposed and the following diagnosis offered:

Specific Diagnosis: Synangia containing 5–9 sporangia; central column extending approximately half the length of the synangium. Sporangia 1.50–1.80 by .20–.45 mm. Dehiscence by a longitudinal cleft along the innermost sporangial wall. Spores monolete, bilateral, measuring approximately 12 × 20 μ; spore walls smooth, with a single longitudinal suture along the concave surface.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1687–1693.

DISCUSSION

The genus *Cyathotrachus* was considered remarkable by its discoverer from the standpoint of its striking similarity to the fructification of the living marattiaceous genus *Christensenia*. This similarity has been pointed out by other authors; the chief difference between the two fructifications lies in the mode of dehiscence, which occurs by means of apical pores in the latter. Notwithstanding its gross similarity to the living genus, Watson was reluctant to assign conclusively his discovery to the Marattiaceae for the reason which he thus expressed:

> I think that two years ago no one would have hesitated to say that it belonged to the Marattiaceae. Now, however, in view of Mr. Kidston's discovery that *Crossotheca*, formerly considered to be Marattiaceous, is really the male fructification of *Lyginodendron*, whose female fructification is, of course, the seed *Lagenostoma*, it seems safer to regard it as of uncertain position, although belonging to either the Ferns or Cycadofilices, and I think most probably to the Ferns. For this reason I have put the word "Fern" in inverted commas in the title.

Although specimens referable to this genus have not been found in numbers sufficient to attract much attention,[13] other authors (Hirmer, 1927; Scott, 1920; Seward, 1910; Arnold, 1947) have remarked on its close similarity to the genus *Ptychocarpus*. The similarity may be noted by a comparison of figs. 11 and 13, the former being a reproduction of Renault's original illustration of *P. unitus* Brongniart. If the central column were removed from the latter, the two fructifications would indeed be morphologically identical; furthermore, discounting the presence of a vascular strand in the central column and the fact that the spores are still contained within the sporangia, Renault's figure might find a favorable comparison with the specimen shown in fig. 15. As a pertinent opinion, we quote Scott (1920), who wrote: "The fructification of *Ptychocarpus unitus* is, however, a good example of a typical Marattiaceous synangium, and affords strong evidence as to the affinities of the plant."

Considering the undeniable morphological similarities between the two genera, it seems that the opinion expressed above should apply to *Cyathotrachus* as well as *Ptychocarpus*. Indeed, it appears that the bulk of the evidence weighs in favor of a marattiaceous affinity for *Cyathotrachus*. Further pertinent discussion will be presented in succeeding pages.

SCOLECOPTERIS Zenker, Linnaea 11:509–512. 1837.

This fructification genus was based upon silicified material from the Lower Permian of Saxony, the type species being *S. elegans*. Although the scope of Zenker's original descriptions was somewhat hampered by the poor quality of preparations available to workers of his time, the generic diagnosis is sufficiently complete that confusion of this fructification with other genera is not likely. The original diagnosis is as follows: "Capsulae hypophyllae non zonatae binae—quinae

[13] The only other specimens reported appeared in Darrah's (1941) treatment of the American coenopterid ferns, in which he reported "sporangia which have *Cyathotrachus* structure."

in unum glomus breviter stipitatum aggregatae, apice longitudinaliter hiantes. Indusium nullum."

The generic name literally means "worm fern" (Greek σκώληξ, worm; πτερίς, fern). The name was proposed in reference to the superficial resemblance of the numerous crowded pinnules to the segmented bodies of a host of maggots! This superficial similarity later caused Geinitz (1872) actually to interpret silicified *Scolecopteris* specimens as fossil millipedes; he named his specimens *Palaeojulus dyadicus* on this account (*Julus* being a modern millipede genus). Subsequent searches for the heads of these "worms" demonstrated the presence of attached fructifications and the errors of his interpretations.

In 1874 Strasburger made a more detailed investigation of Zenker's original material and redescribed the fructifications in a work which has since won acclaim among paleobotanists. This paper includes a critical comparison of the fructifications with those of other ferns and indicates his acceptance of the marattiaceous affinity of *Scolecopteris*.

Grand'Eury (1877) published very brief accounts of two additional species, *S. subelegans* and *S. ripageriensis*, from the Carboniferous of France. Although he attributed an "indusial" structure to *S. subelegans*, its presence is by no means clearly indicated. Furthermore, the two illustrations, which appear in natural size and a magnification of only two diameters, respectively, hardly present a basis for satisfactory comparisons of these fructifications with other species of *Scolecopteris*.

Several years later Renault (1883) described the fructifications of *Pecopteris polymorpha* under the name *Scolecopteris polymorpha*. His well-known drawing of this species, which appears in almost every text-book of paleobotany, shows the synangia arranged in a single series on either side of the pinnule midrib. They are sessile, and are composed of four sporangia each, fused at their inner surfaces to a central column which extends about a third of the distance from the base. The sporangia have long, bristle-like apices. In spite of the sessile attachment of the fructifications and the central column, Renault considered it to be within the generic limits of *Scolecopteris*. This point met with disagreement in 1890 when Schimper removed the fructification genus from *Scolecopteris* and created the new genus *Acitheca* in recognition of the generic significance of the difference between sessile and stalked synangia. Kidston (1925) concurred with Schimper's views.

Scolecopteris was assigned to the suborder Asterotheceae of the Marattiales by Stur, in 1883. The suborder was segregated to include fructifications in which the sporangia are stellately arranged; its original inclusions were the genera *Scolecopteris* Zenker, *Diplazites* Goeppert (*Ptychocarpus* Weiss), *Sturiella* Weiss (*Renaultia* Stur), and *Asterotheca* Presl. The asterothecous affinities of the two additional genera, *Acitheca* Schimper and *Cyathotrachus* Watson, which were not known at the time of Stur's publication, were pointed out by Graham (1934).

The first American addition to the genus *Scolecopteris* was made in 1926 when Hoskins recognized a new species, *S. minor*, from the Pennsylvanian of Illinois.

As evident from the specific name, this species is distinctive in its relatively small size.

In 1932 Scott described an additional species, S. *Oliveri*, based upon silicified specimens from the Permo-Carboniferous of Autun, France. This was followed in 1933 by a paper in collaboration with Holden, in which the foliage of the species was described. The silicifications are apparently the acme of preservation, and the descriptions and illustrations are correspondingly gratifying. The species is quite distinct from others, chiefly in its bilateral spores and the dimensions of the fructifications. Of exceptional interest, however, is the fact that the material was so well preserved that minute studies of such intimate details as epidermal hairs, ramenta, hydathodes, and stomata were possible.

Graham (1934) described the second American species, S. *latifolia*, from the Upper Pennsylvanian of Illinois. This fructification is distinct from ones previously described in its much larger spores (at least twice the diameter of other species known at the time of his publication) and the extremely inflexed, broad margins of the pinnules, from which the specific name was derived. In the same publication he reported specimens which he considered to belong to S. *minor* Hoskins, in spite of noticeably smaller pinnules and other differences, which he attributed to environment.

Andrews (1943) described the species S. *Radforthii* upon the basis of compressions from the McLeansboro formation in Illinois. Although the spores correspond closely in size with those of S. *latifolia* Graham, sporangial dimensions are not in close agreement, and the foliage shows no indication of the broad revolute nature of the latter species.

Following is a list in chronological sequence of the species known prior to this study.

S. *elegans* Zenker, Linnaea 11:509. 1837.

S. *subelegans* Grand'Eury, Acad. Sci. Inst. France, Mem. 24:72–73. 1877.

S. *ripageriensis* Grand'Eury, *Ibid.* 73.

S. *minor* Hoskins, Bot. Gaz. 82:427–436. 1926.

S. *Oliveri* Scott, Linn. Soc. [London] Jour. Bot. 49:1–12. 1932; *Ibid.* 309–321. 1933.

S. *latifolia* Graham, Bot. Gaz. 95:456–458. 1934.

S. *Radforthii* Andrews, Mo. Bot. Gard. Ann. 30:435–437. 1943.

During the past three years, many specimens of *Scolecopteris* fructifications have been studied, with the result that three new species and a tentative new variety are recognized. Furthermore, significant data have been added to our knowledge of S. *latifolia* Graham. The descriptions of this material are presented in the following pages, and at the conclusion of this chapter appears a chart comparing the significant characters of the various species, as far as they are known.

SCOLECOPTERIS LATIFOLIA Graham, emend. Mamay (figs. 17–23).

Numerous fructifications which are thought to be referable to S. *latifolia* have been observed in coal balls from various of the Iowa localities (chiefly Urbandale).

Faulty preservation and lack of associated foliar remains, however, render a positive identification of the fructifications impossible.

In recently collected coal balls from the Mineral, Kansas, locality it has been my good fortune to discover comparatively well-preserved fructifications, complete with foliage, whose identity as *S. latifolia* can hardly be questioned. However, in spite of the close correlation between various characters of our material and those given in Graham's descriptions and illustrations (1934), the Kansas specimens present significant differences which require careful consideration and warrant an emendation of Graham's original specific diagnosis.

The synangia predominantly contain three sporangia, but groups of four are comparatively common, while none with more than four have yet been found (fig. 18). The sporangia are attached at their bases to a common pedicel (fig. 17). No evidence of vascularization of the pedicel has been observed. Above the point of attachment with the pedicel the sporangia of a single synangium are quite free from each other, although in some instances they are so closely appressed that an illusion of a connection is created. There is no central column in the synangium as indicated by Graham.

Individual sporangia vary from .90 mm. to 1.20 mm. in length and from .39 to .34 mm. in width; the width is usually greatest near the base and decreases gradually toward the distal end, resulting in an acute sporangial apex (fig. 17). The outer, or free surfaces, of the sporangial walls are not appreciably thicker than the inner. When seen in transverse sections (fig. 18), the sporangia are roughly triangular, due to the close appression with adjacent ones. Dehiscence occurs, as in all other species of *Scolecopteris*, by means of a longitudinal cleft along the innermost surfaces of the sporangia.

The spore contents of the Kansas material leave much to be desired from the standpoint of preservation. Although the majority of the sporangia are nearly filled with spores, the spores are mostly collapsed or fragmentary and were apparently preserved prior to maturity, judging from the great variability in their sizes. The spores are trilete, the better preserved ones up to 35 μ in diameter. The spore walls are without any distinctive sculpturing, but faint triradiate markings have been seen in a few specimens (fig. 20).

The pinnules are arranged alternately upon the penultimate midrib, and when seen in sections transverse to the midrib have margins which are so inflexed that they nearly form a closed chamber or cylinder (fig. 17). Measured at the "shoulders," the pinnules average 2 mm. in width. This does not, however, embrace the entire width, for if the inflexed margins were flattened out the width would then approach 7 mm. Figure 17 illustrates this aspect of the pinnules very well. Here are shown two pinnules, each bearing two fructifications which are nearly enclosed by the foliar margins. The short pedicel may be seen attaching one of the synangia to the pinnule at the right. The upper surface of the pinnule is composed of an epidermal layer with a relatively thick hypodermis, the two being indistinguishable from each other. The cells of this region are filled with a dense

black substance. The lower epidermis is a very thin layer, probably a single cell thick. Between the upper epidermis and the lower the tissues are not preserved. The midrib is relatively small, and the vascular tissue is not preserved. (The midrib of the penultimate pinnule, however, has been seen to contain a u-shaped vascular strand with the open ends oriented adaxially.) Slightly below the "shoulders" of the pinnule the dense tissues of the upper and lower surfaces merge into a single tissue which composes one-third of either side of the lamina.

As seen when sectioned in the plane parallel to the lamina proper, the pinnules average 3.80 mm. in length and display the typical pecopterid outline (figs. 19 and 23). In fig. 23, the section has intercepted several of the unbranched lateral veins. The several synangia, which are sectioned very near their proximal ends, are seen to be inserted directly below the lateral veins in a single series on either sidé of the midrib. Figure 18, showing a specimen sectioned in a plane somewhat lower than that in fig. 23, illustrates the epidermis and hypodermis with their dense contents. Here we see eleven fructifications sectioned transversely; of these, seven contain only three sporangia each. Proceeding further downward in this series, it soon becomes apparent that we are dealing with a type of pinnule which is unique for the genus *Scolecopteris*. As the upper and lower epidermal layers merge to form the single homogeneous tissue described above and illustrated in fig. 17, this tissue becomes dissected, resulting in an *incised margin* to the pinnule. This is illustrated in fig. 19. Here the essentially pecopterid outline of the pinnule is preserved, but the margin is seen to be composed of not a continuous line of tissue, but of a series of small crescent-shaped segments averaging .50 mm. in length and .15 mm. in width, with the convex surfaces directed toward the midrib of the pinnule. In this figure, the outline of one pinnule is seen extending away from the rachis, with segments of the margins of two adjacent pinnules also present. The discreteness of the marginal lobes is best shown in fig. 21. The lamina proper, with fragments of several longitudinally sectioned fructifications attached, is seen in the upper portion of the illustration. At the lower portion appear the several marginal lobes of the pinnule. They are well-defined, separate bodies with dense cellular contents corresponding exactly to those seen in figs. 17, 18, and 19. Another conspicuous feature are the multicellular hairs attaining lengths of .50 mm., which arise from both the dorsal and ventral surfaces of the marginal lobes. Figure 22, showing a single enlarged lobe (sectioned transversely), illustrates especially well the dense cellular contents and the multicellular hairs.

By serial sections of the Kansas specimens, the following facts pertinent to *S. latifolia* have been established:

1. The lateral veins of the pinnule extend only approximately as far as the "shoulders" of the pinnule. Beyond this point they are indistinguishable, and beginning at approximately the point where they disappear, the lamina becomes dissected, the number of resultant marginal lobes usually corresponding to the number of veins. The margins of the lobes fall in the area between the veins.

2. The fructifications are inserted singly, below and near the ends of the veins; they are accordingly situated very close to the bases of the marginal lobes.

From the above information inferences of phylogenetic interest may be made which will be taken up in detail later in this paper.

In several respects the Kansas specimens correspond sufficiently with the type description that their identity with S. *latifolia* is obvious. They concur exactly in the dimensions of the fructifications, numbers of sporangia in the synangia, and in the shape and total width of the pinnules, as seen in transverse sections. A completely satisfactory comparison of the spores is not possible, but they are alike in having triradiate markings and smooth exines. Furthermore, the measurements of the spores of our material agree with Graham's specifications.

Graham described a central column in the synangium. This I attribute to a misinterpretation on his part. Such a structure, although shown in his line drawing (fig. 7 of his paper), is not apparent in the photograph which appears in his figure 27, or in his original slides.[14] In his illustration and the Kansas specimens the closely appressed walls of adjacent sporangia superficially seem to be fused organically. Minute examination of the Kansas specimens has invariably proved that this is not the case, however. If a central column were present, the fructification would indeed be beyond the limits of *Scolecopteris* and would represent a fructification intermediate between the genera *Scolecopteris* and *Acitheca*.

The dissected margin of the pinnule was not mentioned by Graham. This feature is not clearly seen in Graham's slides due to inferior preservation and absence of a section comparable to that shown in fig. 19. While it is not my intent to confuse the nomenclature of the genus, it seems that the results of this study necessitate an emendation of Graham's concept of S. *latifolia*, with particular reference to the central column and the margination of the pinnules.

Emended Specific Diagnosis: Synangia consisting of usually 3, sometimes 4, sporangia. Sporangia with acute apices and ranging from .90 to 1.2 mm. in length and from .34 to .39 mm. in width, attached basally to a short synangial pedicel, but free above; outer surfaces of walls not appreciably thicker than the inner; dehiscence by means of a longitudinal cleft along the innermost sporangial wall. Pinnules averaging 3.80 mm. in length and with total widths averaging 6.50 mm., strongly inflexed and deeply incised on the margins, with a single synangium inserted near the base of each marginal lobe and directly beneath a lateral vein; lobes averaging .50 mm. in width, with multicellular hairs borne on both surfaces. Spores spherical, to 35 μ in diameter, with trilete scars and otherwise smooth exines.

Age: Fleming coal, Cherokee shale.

Locality: Mineral, Kansas.

Type Slides: #1694–1697.

[14] Graham's type slides of S. *latifolia* were made available for this study through the kindness of Dr. R. M. Kosanke, of the Illinois State Geological Survey.

SCOLECOPTERIS **iowensis**, sp. nov. (figs. 24–28).

Several small Urbandale coal ball slabs (WCB 511, 515, 517, 518) were found to contain an abundance of these fructifications, in many cases attached to the pinnules. The color and texture of the slabs WCB 511, 515, and 517 indicate that they probably were cut from the same coal ball, but this cannot be verified since they were sent to this laboratory already sawed.

The synangia consist of four, five, or most commonly six, elongate sporangia. They are arranged circularly and are attached at their bases to a common pedicel. The fructifications are inserted in a single or sometimes double series on each side of the pinnule midrib. The synangia average about 1 mm. in length (including the pedicel), and about .90 mm. in diameter, this dimension being dependent upon the extent to which the sporangia have spread radially. The individual sporangia average about .90 mm. in length and .33 mm. in width, with the greatest diameter usually being very near the base. Although attached at their bases to a common pedicel, the sporangia are separated throughout their entire lengths. In longitudinal section (fig. 27), they are seen to taper toward their distal ends, terminating in bluntly acute apices. The sporangial cavity, however, is roughly ovoid in longitudinal section, the sporangial apex being formed by the elongate wall cells and not representing a continuation of the cavity. The cells of the sporangial walls are approximately 30 μ in diameter and 150 μ in length.

Although preservation of the cells is not altogether complete, a sharp contrast may be noted between the outer and lateral walls of the sporangium (fig. 26). The outer walls are thicker, consisting of two or three layers of cells which have thickened walls and usually contain a dense black substance; the lateral walls, on the other hand, contain only one layer of cells which lack these thickened walls and black contents. In all the specimens examined, the cells of the lateral sporangial walls are lacking the cell wall on the side facing the adjacent sporangium (fig. 26). This condition, together with the fact that the sporangia appear to be laterally flattened in transverse section, suggests that the sporangia were probably very closely appressed prior to maturity; the separation of the sporangia upon reaching maturity very likely ruptured the walls of these cells, explaining their absence in our specimens.

Dehiscence was accomplished by means of a longitudinal slit along the innermost surface of the sporangial wall (fig. 28). The majority of the sporangia shown in this section exhibit dehiscence slits and have shed their spores.

The pedicels average about .15 mm. in length and .20 mm. in width. Their component cells are of thin-walled parenchymatous nature, measuring about 30 μ in diameter and 45 μ in length (fig. 27). There is no evidence of vascularization of the pedicel.

The spores constitute the most distinctive single feature of this fructification. In size they exceed those of all other species of *Scolecopteris*, attaining diameters of 80 μ, but averaging about 65 μ. Distinct triradiate markings and delicate reticula-

tions of the exine are present (fig. 25). The spore output was relatively small, probably not exceeding 100 per sporangium.

The pinnules have strongly inflexed margins. Normally they average about 3.50 mm. in width and 7 mm. in length, but if the inflexed margins were to be flattened out the width would be increased to about 5 mm. The structure of the pinnule is fairly well known. Figure 24 shows it to possess a strong midvein containing a terete vascular strand surrounded by large thin-walled cells, probably parenchymatous. A well-developed palisade layer is present. The upper epidermis is heavily cuticularized; the lower epidermis is also, but to a lesser extent. The mesophyll tissue lying between the point of insertion of the synangia and the margin of the pinnule consists of flat plate-like cells whose greater axes parallel the plane of the pinnule surface.

The specimen represented in fig. 24 indicates that the synangia were ordinarily borne in a single series on each side of the midvein. However, instances of departure from that condition have also been noted. Figure 28 shows a section taken through the midvein of a pinnule in a plane parallel to the plane of the lamina. Here is shown a lateral vein departing from the midrib, with two distinct rows of synangia lying parallel to the midvein. These two rows of synangia might be interpreted as belonging to two separate adjacent pinnules, but thorough investigation of this and other comparable specimens reveals that the synangia of one row are much too closely appressed with those of the other to accommodate the two inflexed pinnule margins which otherwise would have occupied the position between rows. This would indicate, then, that a single series of synangia on each side of the midvein was not always the case, some of the pinnules apparently having borne two rows of fructifications on each side.

In consideration of the spores alone, this fructification appears to be a distinct species of *Scolecopteris*. Spores of this species are seen to reach diameters of 80 μ, while those of all other species are much smaller, with the exception of S. *latifolia* and S. *major* (description on following pages). In S. *latifolia* they are known to attain a maximum diameter of 35 μ; furthermore, the predominance of trilocular synangia, the sporangial dimensions, and unthickened outer sporangial walls of S. *latifolia* are in striking contrast to the usually 6-locular synangia, smaller sporangia and unequally thickened sporangial walls of S. *iowensis*. The specific distinctions between S. *iowensis* and S. *major* (discussed below) leave no alternative but to recognize this fructification as a new species. The name S. *iowensis* is proposed with reference to the type locality, and the specific characters are summarized in the following diagnosis:

Specific Diagnosis: Synangia borne in single or double series on each side of midvein and consisting of 4, 5, or, most commonly 6, sporangia. Sporangia free laterally, attached basally to a common pedicel, averaging approximately .35 mm. by .90 mm.; outer surfaces of walls thickened, inner surfaces thin; dehiscence by a longitudinal cleft along the innermost surface of the sporangial wall. Spores round, 65–80 μ in diameter, with triradiate scars and reticulate exines. Pinnules

averaging 7 mm. in length, normally about 3.5 mm. wide, but 5 mm. wide if unrolled.

Age: Des Moines Series of the Pennsylvanian.
Locality: Urbandale Mine, Iowa.
Type Slides: #1698–1702.

SCOLECOPTERIS MINOR Hoskins, var. **parvifolia**, var. nov. (figs. 29–33).

This extremely small fructification with its proportionately small supporting pinnules has proven to be the most abundant and widely distributed form of *Scolecopteris*. Its presence was first noted in coal balls 431 and 445, from the Urbandale Mine in Iowa, and it is chiefly on this material that the following description is based. Since the beginning of this study, however, petrifactions from several other localities have been collected and sawed, and fructifications which correspond exactly with the original material have been found in coal balls from Lynnville, Ind., Berryville, Ill., Mineral, Kans., and in one tiny fragment from Shore, Lancashire, England.

An outstanding specimen consisting of the greater portion of an ultimate rachis and several attached pinnules was found in WCB 431. Although the original saw-cut sectioned the specimen slightly obliquely to the plane of the lamina, it clearly illustrates the nature of the pinnules and their fructifications.

The synangia usually contain only four sporangia, but groups of five are not uncommon and one synangium with six was found. The synangia average about .70 mm. in diameter and .65 mm. in length, including the pedicel. They are always arranged in a single series on each side of the midvein, on the dorsal surface of the pinnule. The individual sporangia are ovoid in longitudinal section, averaging from .56 to .60 mm. in length and about .35 mm. in diameter. In longitudinal section (fig. 33) the sporangial apices are seen to be more blunt than those of *S. iowensis*. Here again, the apex is formed by elongate wall cells and does not represent a continuation of the sporangial cavity. The sporangia are grouped about the common pedicel, which in this species superficially resembles a very short central column, due to the slightly oblique basal attachment of the sporangia. Basally the sporangia are closely appressed to each other (not organically fused, however); for the greater part of their lengths the lateral walls are entirely free from each other.

The outer sporangial walls are thickened, usually entailing two or more layers of cells with very heavy walls. The inner walls contain only a single layer of cells whose walls are not thickened as those of the outer wall cells. Dehiscence was accomplished by means of a longitudinal cleft along the innermost surface of the sporangial wall. The transverse aspect of dehiscent sporangia is shown in fig. 31.

The pinnules of this species are much smaller than those of other species. They seldom exceed 4 mm. in length, averaging about 3 mm.; width averages about 1.75 mm. The margins are strongly inflexed, however, and if they were flattened out the width would be increased to about 2.50 mm. The nature of the pinnules is

shown in fig. 32. This section has been cut through the lamina on one side of the midrib and through the attached synangia on the other side. The strong ultimate rachis may be seen with the pinnule midvein departing from it. Lateral veins are seen departing from the pinnule midvein. There are five synangia and five lateral veins in evidence, their relative positions indicating that the fructifications are borne directly beneath the veinlets. There is no evidence of incision of the margins. Figure 29 is a transverse section of a pinnule, further illustrating the strongly inflexed condition of the margins. Also shown is a strong midvein, although faulty preservation precludes a detailed study of the vascular tissue. Palisade tissue seems to be lacking, and the epidermal layers show no apparent cuticularization. The uniseriate insertion of the fructifications is shown in fig. 32.

The spores are badly crushed in the majority of the specimens. There is, however, a triradiate scar present, although the exine is without any additional markings. The spores are spherical, averaging approximately 15 μ in diameter (fig. 30).

Spore and sporangial dimensions distinguish this fructification from S. *latifolia*, S. *major*, S. *elegans*, and S. *iowensis*, while the morphology of the spores serves in itself to separate it from S. *incisifolia* (description to follow) and S. *Oliveri*. Had this study been limited to inspections of only a few specimens, they might have been referred to S. *minor* because of the strong resemblance. However, in view of the constancy of the cited dimensions in numerous specimens from several widely separated localities in America and one in England, the smaller sporangia and pinnules appear to constitute a reliable basis for recognizing this fructification as a small varietal segregate of S. *minor*. The characters of S. *minor* var. *parvifolia* are summarized in the following diagnosis:[15]

Varietal Diagnosis: Synangia borne in a single series on each side of the midrib, and consisting of 4, sometimes 5, sporangia. Sporangia ovate, with blunt apices, averaging approximately .58 mm. in length, .35 mm. in width, closely appressed at the bases, but entirely separate for the greater part of their lengths; outer surfaces of walls thickened, inner surfaces thin; dehiscence by means of a longitudinal cleft along the innermost surface of the sporangial wall. Pinnules with strongly inflexed margins, averaging 3 mm. in length, normally about 1.75 mm. in width but 2.60 mm. if unrolled. Spores round, averaging 15 μ in diameter; walls with triradiate scars and otherwise smooth exines.

Age: Des Moines Series of the Pennsylvanian; the Great Coal Ball Horizon.

Localities: Urbandale Mine, Iowa; Berryville, Ill.; Lynnville, Ind.; Mineral, Kans.; Shore, Lancashire, England.

Type Slides: #1703–1708.

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[15] Graham (1934) described fructifications which correspond exactly with S. *minor* var. *parvifolia* in every aspect. He felt, however, that the size factor was one which could have been induced by environment and referred the specimens to S. *minor*. The constancy of the small size of this variety having been demonstrated by its widespread distribution, it seems probable that the specimens he described should be referred to S. *minor* var. *parvifolia*.

SCOLECOPTERIS **incisifolia**, sp. nov. (text-fig. 1; figs. 34–41).

Several isolated fragments of this fructification, including three nearly complete supporting pinnules, were found in WCB 431, from the Urbandale Mine. While these specimens represent various stages of maturity and accordingly display greater variation of size, it was possible to correlate them by comparisons of the spores and the oddly incised foliage.

In one specimen in which the pinnule is sectioned at right angles to the plane of the lamina and parallel to the midrib (fig. 34), several synangia are seen sectioned transversely. These were apparently preserved prior to spore formation, as neither spores nor lines of dehiscence are noticeable. The extreme thickness of the outer walls of the sporangia is striking as compared to the thin inner walls. Of the four synangia shown here, three are trilocular, the fourth quadrilocular. An inspection of all the specimens available shows the quadrilocular synangia to be slightly more numerous than the trilocular, while synangia with more than four sporangia have not been observed.

In mature fructifications (fig. 41) the sporangia are intimately appressed to each other, with the result that the lateral sporangial walls are flattened while the outer walls are rounded. The inner, or lateral, walls of the sporangia are apparently only a single cell thick; the outer composed of at least two layers of cells. The sporangia shown in this illustration display maximum diameters of about .36 mm., the entire synangium not exceeding .80 mm. in diameter. Although this specimen does not illustrate dehiscence, others have shown it to occur by a longitudinal cleft along the innermost portion of the wall of each sporangium.

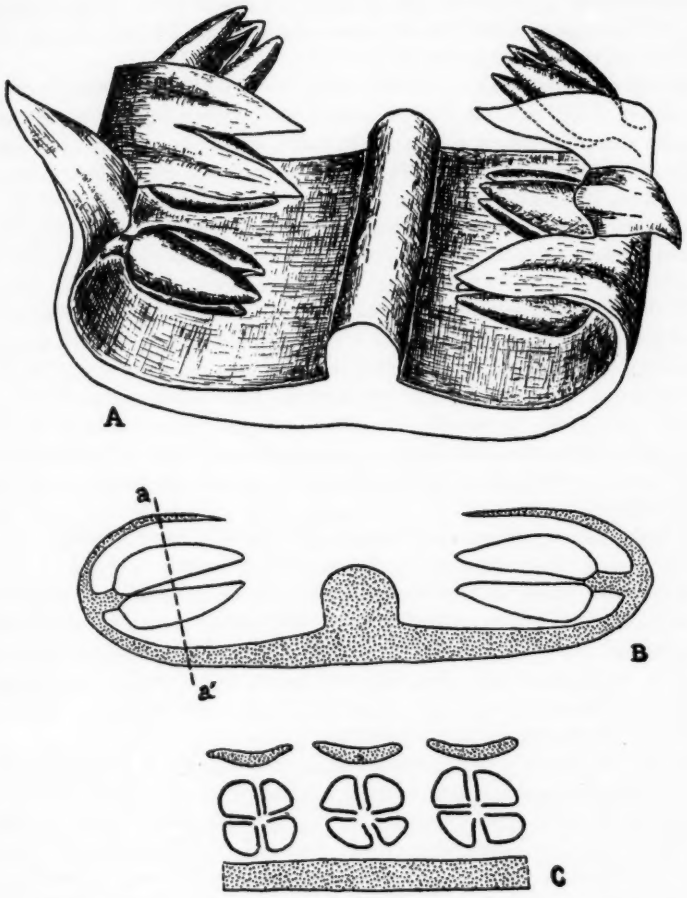
Figure 35 illustrates two immature synangia, sectioned longitudinally, from the same pinnule on which the fructifications shown in fig. 34 were borne. The foliar tissue is seen at the top of the figure and the synangia are attached to it by stout pedicels. The outstanding feature of these pedicels lies in their possession of vascular strands, each consisting of several small tracheidal elements measuring approximately 17–22 μ in inside diameter. These strands originate from the lateral veins of the pinnule, and are the only instances in which vascularization of synangial pedicels has been observed during this investigation. The pedicels shown here are about .22 mm. wide and .30 mm. long. The sporangia, which measure about .45 mm. in length and .17 mm. in width, are attached to the pedicels only by their basalmost portions.

A more mature synangium is shown in fig. 40, in which three sporangia are seen sectioned longitudinally and slightly obliquely. Their shape is roughly ovoid, with no appreciable tapering of the distal end (other specimens, however, show the sporangial apices to be typically more acute). Although the inner walls of the sporangia are closely appressed, this does not represent actual organic fusion, as observations of other specimens have proven the sporangia to be entirely free from each other throughout their lengths. The sporangia of this synangium are .45 mm. in length and .20 mm. in width. Others with lengths reaching .75 mm. have been seen, however.

The spores (fig. 39) are small, reaching 22 μ in length and 14 μ in width. They are of the monolete, bilateral type. The two spores shown here are taken from one of the synangia shown in fig. 41. The spore walls are entirely devoid of tetrad scars or other markings of the exine, and their most conspicuous feature lies in their thickness, most clearly shown in the spore at the left. The spores within a single sporangium vary in length from 18 to 22 μ, and the pronounced thickness of the spore walls usually occurs in only the largest spores, which are interpreted as the most mature.

The major point of interest concerning S. *incisifolia* lies in the supporting pinnules (figs. 37 and 38). Figure 37 shows a pinnule sectioned parallel to the plane of the lamina but slightly beneath it, with the result that only the inflexed marginal portions appear. Since the color contrast between the actual specimen and the surrounding matrix was not great enough to allow for satisfactory photographic reproduction, the accompanying line drawing is offered (fig. 38). This pinnule is 5 mm. long and nearly 2 mm. wide. A portion of the midrib is seen extending proximally for some distance from the distal end. That the margins of the pinnule are strongly inflexed is shown by the fact that the margin at the upper portion of the photograph appears as a continuous line of tissue connecting both ends of the pinnule. Of particular interest here is the undulate *inner* surface of this margin, the outer surface appearing nearly smooth. This results in alternating thick and relatively thin portions of the margin. These are, in fact, the lateral veins, as each thickened portion is seen under high magnification to contain a very small vascular bundle. At point *a*, a single synangium is seen lying in essentially the same plane as the lamina proper. Proceeding now to the opposite margin (lower portion of the illustration), we see that the constrictions of the tissues lying between the veins are further accentuated, and that the margin has become incised at about the center, with two marginal lobes appearing as discrete bodies (point *b* in the line drawing). This fructification resembles S. *latifolia* in that the supporting pinnule has an incised margin, with the fructifications borne near the bases of the lobes.

A correlative inspection of fig. 34 and figs. 37 and 38 shows that the former represents a section taken parallel to the midrib, but very close to the margin and in a plane at right angles to that of figs. 37 and 38. Thus while the synangium seen in figs. 37 and 38 is sectioned longitudinally, those in fig. 34 are transversely sectioned. Here the lamina of the pinnule appears at the upper part of the photograph. Directly beneath this lie the synangia, and below them are the marginal lobes which have been so strongly inflexed that they too are sectioned transversely. It is of importance to note here that *one lobe* lies directly opposite each fructification. These are rather sausage-shaped in transverse section, with the convex surfaces directed toward the synangia. They average 90 μ in thickness and approximately .34 mm. in width. A single lobe, sectioned transversely, is shown in fig. 36. Since sections comparable to the one seen in fig. 17 *(S. latifolia)* have not been found in this material, the length of these lobes is not known. In one instance,



Text-fig. 1. Reconstruction of *Scolecopteris incisifolia: A* shows the gross aspect of the lower surface of a portion of a fertile pinnule; *B*, a transverse section of the pinnule; *C*, a section cut through plane *a-a'* of *B* (this approximates the section illustrated in fig. 34).

however, a lobe has been observed nearly 1 mm. in length. These structures are further illustrated in fig. 41.

Although several specimens of S. *incisifolia* show incision of the foliage essentially like that of S. *latifolia*, the marginal lobes of S. *incisifolia* are more strongly inflexed than those of S. *latifolia*, the tips pointing almost directly toward the midrib of the pinnule. The synangia are inserted one near the base of each marginal

lobe and occupying a position directly beneath a lateral vein. Like the marginal lobes, the synangia are also pointed toward the midrib. The morphology of this fructification is presented in text-fig. 1.

From the standpoint of morphology of the pinnules, S. *incisifolia* appears to be most closely related to S. *latifolia*. However, spore morphology of the two appears sufficient to separate them as two entirely distinct species. Spores of S. *latifolia* are relatively large and trilete, while those of S. *incisifolia* are small and monolete. Furthermore, the thick hypodermal layer and hirsute indument of S. *latifolia* are absent in our species. Also, the sporangial walls of S. *latifolia* are nearly equal in thickness, while those of S. *incisifolia* are noticeably thickened on the outer surfaces.

Of the remaining known species of *Scolecopteris*, S. *Oliveri* is the only other one with monolete spores, and it differs from S. *incisifolia* in the following respects: Its pinnules, although minutely toothed, cannot begin to approach the deeply incised condition of our species; the spores of S. *Oliveri* have rugose exines, while those of S. *incisifolia* are smooth; the hirsute and ramental indument of S. *Oliveri* is lacking in our species. For these reasons, in addition to the difference in dimensions of the fructifications, we feel justified in recognizing our specimens as distinct from S. *Oliveri*.

Although the material upon which this description is based is inferior in preservation to any other described specimens of *Scolecopteris*, and the number of specimens found as yet is not great enough to provide as complete an insight into the morphology as has been realized in the study of other species, the small bilateral spores and the incised foliage comprise a combination of characters not yet known to exist in any other species. For this chief reason, these fructifications appear to constitute a distinctly new species of *Scolecopteris*. The species is named with reference to the margination of the pinnules.

Specific Diagnosis: Synangia consisting of 4, sometimes 3, sporangia reaching .75 mm. in length and .36 mm. in width; sporangia blunt to acute at the apex, attached basally to a stout synangial pedicel, but free above; outer surfaces of walls thicker than the inner; dehiscence by means of a longitudinal cleft along the innermost surface of the wall. Pinnules averaging 5 to 6 mm. in length and 2 mm. in width (exclusive of the strongly inflexed margins); margins deeply incised, with a single synangium inserted near the base of each marginal lobe and directly beneath a lateral vein; lobes averaging .34 mm. in width. Spores monolete, to 22 μ long and 14 μ wide, with thick walls and smooth exines.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1709–1712.

SCOLECOPTERIS **major**, sp. nov. (figs. 42–46).

This description is based upon the fructification content of a single small coal-ball slab from the Urbandale locality. Although the slab originally measured only

approximately 6 × 6 × 1 cm., it was found to contain numerous fructifications which are specifically distinct from other previously described species of *Scolecopteris*, and in an excellent state of preservation. The spores, however, are for the most part poorly preserved, and recognizable foliar remains to which the fructifications might be attributed are entirely lacking.

The synangia are composed of only four sporangia, except in one case where a single synangium with five sporangia was observed. The length of the synangia reaches 3 mm. (including the pedicel). In transverse section the fructifications are roughly circular, attaining diameters of about .90 mm. In all cases, the fructifications, although apparently mature and almost devoid of spores, have maintained a close appression between adjacent sporangia.

The pedicel is short and broad, measuring approximately .35 × .60 mm. in the specimens in which this portion was still intact (fig. 44). It is possible, however, that the length may have been greater, since the actual attachment to foliar tissue has not been observed. The pedicel is not known to contain vascular elements.

Individual sporangia are remarkable for their extreme length. They average more than 2 mm. long, and one specimen has been found which measures 2.9 mm. long. In transverse section they appear much as the four equal segments of a circle, with the two lateral walls of each sporangium creating an angle of approximately 90 degrees. The width of the sporangia is greatest near the proximal ends, reaching .60 mm.; it gently decreases toward the distal ends, resulting in very acute apices (figs. 43 and 44). The outer walls of the sporangium are at least two cells thick, the thickness increasing toward the distal ends. The lateral or inner walls are composed of only one layer of cells, elongate in the direction of the long axes of the sporangia. The cells of the inner sporangial walls have lost their walls on the surfaces facing adjacent sporangia. In this respect the synangia, as seen in transverse section, resembles *S. iowensis* except for the number of sporangia contained. The transverse aspect of the fructifications is illustrated in fig. 42. Here the longitudinal slits of dehiscence may be noted as openings at the innermost portions of the sporangial walls (i.e., at the right angle created by the two lateral walls).

Multicellular hairs reaching 300 μ in length are found on the outer sporangial walls. They are most thickly aggregated at the apices of the sporangia, their number decreasing gradually toward the bases. In fig. 46 two such hairs are seen in high magnification.

The majority of our specimens were preserved after the spores had already been shed. However, several sporangia with portions of their spore masses intact have been found. In general, the spores are round and large for this genus, the diameters ranging from 45 to 55 μ. The exine is characterized by a rather coarse reticulate sculpturing, and triradiate ridges are present in the better-preserved specimens (fig. 45).

COMPARISON OF THE VARIOUS SPECIES OF *SCOLECOPTERIS*

	Average dimensions of sporangia	Number of sporangia per synangium	Nature of sporangial walls	Dimensions of pinnules	Pinnule margins	Arrangement of synangia	Spore dimensions, sculpturing
S. *elegans* Zenker	.40 × .90 mm.	Usually 5	Thickened outer surfaces; inner surfaces thin	3.50–4.00 mm. long; 1.50–1.70 mm. wide	Entire	Single series on each side of midvein	10 μ diameter; triradiate scars, smooth exines
S. *Oliveri* Scott	.44 × 1.32–1.40 mm.	Usually 4, sometimes 3 or 5	Thickened outer surfaces; inner surfaces thin	6 mm. long; 2.70 mm. wide	Minutely toothed	Single series on each side of midvein	Bilateral, with greatest dimension 18 μ; exine rugose
S. *latifolia* Graham	.34–.39 × .90–1.20 mm.	3 or 4	No thickening of outer surface	3.80 mm. long; 7 mm. wide if unrolled	Deeply incised	Single series on each side of midvein	35 μ diameter; triradiate scars, smooth exines
S. *Radforthii* Andrews	.25 × .70 mm.	3 or 4	?	3 mm. long; 2 mm. wide	Entire	Single series on each side of midvein	32 μ diameter; triradiate scars, smooth exines
S. *minor* Hoskins	.28 × .70 mm.	Usually 4, sometimes 5, rarely 6	Thickened outer surfaces; inner surfaces thin	6–7 mm. long; 3.30 mm. wide	Entire	Single series on each side of midvein	17 μ diameter; no markings
S. *minor* var. *parvifolia* Mamay	.35 × .58 mm.	Usually 4, sometimes 5, rarely 6	Thickened outer surfaces; inner surfaces thin	3 mm. long; normal width 1.75 mm.; 2.60 mm. if unrolled	Entire	Single series on each side of midvein	15 μ diameter; triradiate scars, smooth exines
S. *iowensis* Mamay	.35 × .90 mm.	4, 5, usually 6	Thickened outer surfaces; inner surfaces thin	7 mm. long; normal width 3.5 mm.; 5 mm. if unrolled	Entire	Single *or* double series on each side of midvein	65–80 μ diameter; triradiate scars; reticulate exines
S. *major* Mamay	.50 × 2.10–2.90 mm.	Usually 4, rarely 5	Thickened outer surfaces; inner surfaces thin	?	?	?	45–55 μ diameter; triradiate scars; irregularly reticulate exines
S. *incisifolia* Mamay	.33 × .75 mm.	3, usually 4	Thickened outer surfaces; inner surfaces thin	5–6 mm. long; 2 mm. wide (exclusive of the inflexed margins)	Deeply incised	Single series on each side of midvein	Bilateral, 22 × 14 μ; smooth exines

Although associated foliar remains are not distinguishable, these fructifications, judging from their general orientation, seem to have been preserved in their natural position. They are nearly all oriented in the same direction and very closely crowded (fig. 42). For this reason it seems safe to assume that these fructifications, like those of S. *iowensis*, were borne in more than one series on each side of the midrib of the pinnule.

A comparison of S. *major* with the other known species of *Scolecopteris* reveals several significant differences, the most notable one being the size of the sporangia. The species most closely approaching S. *major* in sporangial dimensions is the English species S. *Oliveri* Scott. However, the average difference in length of sporangia is approximately 1 millimeter. In addition, the small bilateral spores of S. *Oliveri*, in contrast to the large trilete spores of S. *major*, lend much further weight to a specific distinction between the two.

Of the remaining species of *Scolecopteris*, none approaches S. *major* in size. The sporangium is up to 1.6 mm. longer than that of any other species, which constitutes a large difference in consideration of the generally small size of the fructifications. In spore size, S. *major* seems to occupy a position intermediate between S. *latifolia* Graham and S. *iowensis*. Although the spores are somewhat smaller than those of S. *iowensis*, from the standpoint of morphology and exine sculpturing, they correspond more closely to those of that species. It seems indeed that the closest relationship of S. *major* lies with S. *iowensis*. As has been previously pointed out, single sporangia of the two species appear extremely similar as seen in transverse section. Furthermore, if the assumption that the synangia of S. *major* were borne in more than a single series on each side of the midvein should ultimately be proven to be a correct one, the relationship between the two species will be materially strengthened. However, the presence of hairs on the fructification, the almost exclusive predominance of synangia with only four component sporangia, and the great size of S. *major* serve as sufficiently distinctive characters to warrant its recognition as a separate species. The specific name S. *major* is proposed, in reference to the large size of the fructifications.

Specific Diagnosis: Synangia consisting of 4, rarely 5, sporangia basally attached to a short pedicel. Sporangia from 2.10 to 2.90 mm. long, averaging .50 mm. in width; outer walls thickened, inner walls thin; dehiscence by means of longitudinal clefts along the inner sporangial wall; multicellular hairs reaching 300 μ in length produced on outer sporangial walls. Spores round, from 45 to 55 μ in diameter, with triradiate ridges and coarsely reticulate exines.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1713–1717.

Eoangiopteris Andrewsii, gen. et sp. nov. (text-fig. 2; figs. 47–53).

The marattiaceous fructifications dealt with thus far in this paper are those which display radially symmetrical arrangement of the sporangia. The opinion expressed by various authors that this type of fructification represents the archetype in the Marattiaceae has indeed been strengthened by the results of this study. There is no apparent reason to doubt the validity of such an opinion, considering the great predominance of radial sori in the Carboniferous rocks in which the oldest known members of the Marattiaceae are found.

At this point it seems desirable to present a cursory survey of the living Marattiaceae from the standpoint of soral morphology. Of the seven living genera of this family, only one produces radial sori *(Christensenia)*. All other living genera produce fructifications which display linear or bilateral symmetry. The predominance of linear sori among the living Marattiaceae, as opposed to the predominance of radial sori among the Carboniferous representatives of the family, poses the following questions: When did the linear sorus first appear on the scene? How did it evolve? It is known that the linear sorus was already well developed by Triassic times (*Danaeopsis* Heer; *Marattiopsis* Schimper), and the presence of the genera *Danaeites* Goeppert and *Parapecopteris* Grand'Eury in the European Coal Measures indicates a very early origin for this type of fructification.

In the genus *Eoangiopteris* we find a fructification with linear arrangement of the sporangia, but with certain characters strongly reminiscent of *Scolecopteris*. Whether or not it represents the actual ancestral type from which the linear sori of certain of the living marattiaceous genera were derived cannot be conclusively stated at this time. It appears to represent a step in that direction, however, and the matter will be discussed in detail in the phylogenetic section at the end of this paper.

Numerous scattered fragments of this fructification have been found in coal balls 437A, 437B, 442, 500, 501, 502, 516, 678, 679, and 680, of the Washington University collection. These coal balls are all from the Urbandale mine. While the majority of the fragments studied consist of only a single sorus, six specimens have been found which contain more or less complete fertile pinnules (WCB 437A, 442, 501, 502, 679).

Although *Eoangiopteris* lacks the predominant radial sori such as found in the fossil genera *Scolecopteris*, *Ptychocarpus*, and *Cyathotrachus*, it agrees structurally with those living marattiaceous genera whose fructifications are linear and free-sporiangiate *(Archangiopteris, Angiopteris,* and *Macroglossum)*.

The number of sori produced by a single pinnule ranges from 12 to 18. They lie closely spaced and parallel to each other on the dorsal surface of the pinnule, extending from the midrib as far as the inflexed margin. Their linear axes create an angle of approximately 40 degrees with the midrib, the angle of divergence from the perpendicular being toward the apex of the pinnule. By serial peels of the specimen found in WCB 442, it has been established that the sori lie directly beneath and parallel to the lateral veins.

The sori are attached to the pinnule by fleshy receptacles (figs. 48, 51) composed of undifferentiated isodiametric cells averaging 75 μ in diameter. Figure 51 represents a sorus sectioned through its long axis in the plane parallel to the long axes of the sporangia; here the receptacle is shown to be approximately half as deep as the length of the sporangia, with the point of attachment to the pinnule somewhat shorter than the total length of the sorus, which ranges from .90 to 1.35 mm. The sori average about .45 mm. in width. The receptacle is not vascularized.

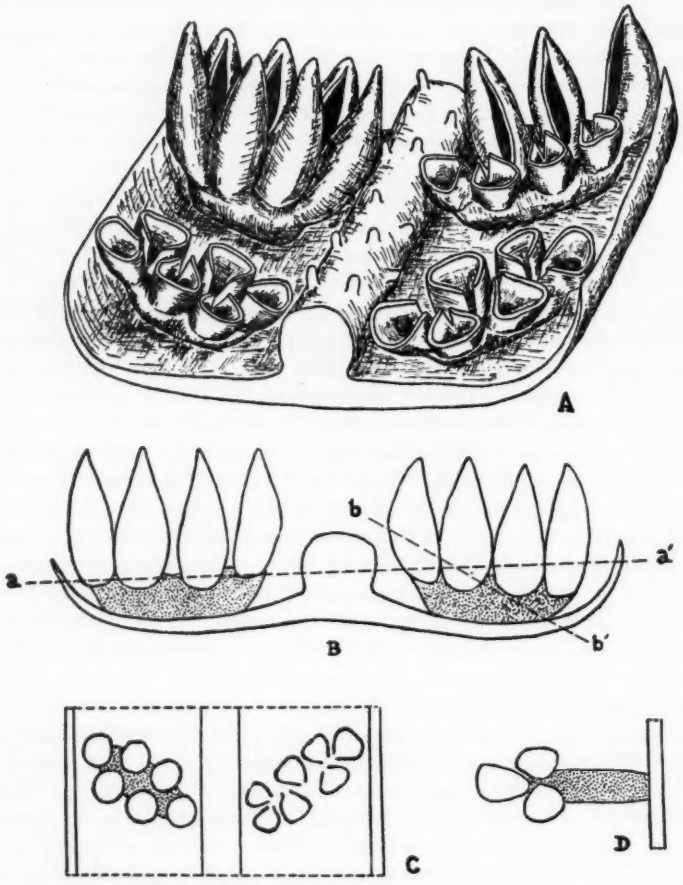
The number of sporangia in the sorus ranges from five to eight, the sori with fewest sporangia being found nearest the distal end of the pinnule. The bases of the sporangia are shallowly immersed in the tissue of the receptacle, but beyond this point of attachment there is no organic connection between adjacent sporangia. A transverse section through the basal portions of the sporangia (fig. 49) shows them to be oval and approximately .25 mm. in diameter, with the receptacular tissue distinguishable between sporangia. A section taken above the point of attachment to the receptacle (fig. 50) shows the sporangia to be roughly triangular in transverse section; in longitudinal section (fig. 51) they are elongate and pyriform, with the greatest width near the point of attachment to the receptacle. In length the sporangia range from .75 to .90 mm., those in the center of the sorus being slightly longer than those at either end. The sporangia of a single sorus are arranged in two rows, each containing up to four sporangia. The rows are either directly opposed or slightly enmeshed in each other, much as the teeth of two gears.

Although preservation of the sporangial walls is not as complete as desirable, it is evident that they are composed of at least two layers of cells. The outermost cells are thick-walled and contain a dense black substance very similar to that observed in the corresponding tissue of *Scolecopteris iowensis*. The inner cell walls are usually thinner than the outer.

Dehiscence (fig. 50) occurs by means of a longitudinal cleft along the innermost wall of the sporangium, the opening extending from the apex of the sporangium to its point of attachment. In details of dehiscence and cellular structure of the sporangial walls the sporangia of *Eoangiopteris* are strongly reminiscent of those of *Scolecopteris iowensis*—so much so, in fact, that single isolated sporangia of the two fructifications would scarcely be distinguishable, discounting the slight discrepancy in size.

Most of the spores are badly crushed, but their salient features have been determined from a few well-preserved specimens. The spores are spherical, with quite thick walls, and range from 45 μ to 60 μ in diameter. The exine shows faint triradiate ridges, but its outstanding feature lies in the nature of the sculpturing. In fig. 52 the exine is seen to be marked by numerous closely spaced, roughly circular pits averaging 4 μ in diameter. The spore output was apparently low, each sporangium having produced a maximum of approximately a hundred spores.

The pinnules range from 7 to 9 mm. in length and from 2.50 to 3 mm. in width. The distal ends are usually somewhat narrower than the proximal. The



Text-fig. 2. Reconstruction of *Eoangiopteris Andrewsii: A*, lower surface of a portion of a pinnule with four synangia attached, the two lower synangia having been transversely sectioned; *B*, transverse section through the pinnule and two synangia, receptacle shaded; *C*, left, a section of synangium taken through plane *a-a'* of *B* (approximately same sectional plane as shown in fig. 49); *C*, right, approximately the section shown in fig. 50; *D*, section through plane *b-b'* of *B* (approximately the same as shown in fig. 48).

margins are strongly inflexed, appearing as a more or less continuous line of tissue surrounding the fructifications when seen in sections that have been made in a plane parallel to and below that of the lamina. In the light of our present knowledge of the fossil Marattiaceae we may conclude that these pinnules represent the ultimate divisions of a several-times compound frond belonging to the *Pecopteris* group. Further evidence in support of this opinion is seen in the vascular anatomy of the specimen shown in fig. 53. This represents the midrib of a pinnule, sectioned transversely. The outermost tissue consists of large collenchyma-like cells, with a few outstandingly large ones, possibly of secretory nature, interspersed among them. The inner zone consists of several layers of smaller, thin-walled cells surrounding a horseshoe-shaped vascular strand (fig. 53a) whose open ends point adaxially. The shape of the vascular strand suggests this pinnule to be the ultimate division of a *Stipitopteris* or some closely allied psaronean petiole containing a horseshoe-shaped leaf trace.

A few multicellular hairs, ranging to .20 mm. in length, have been observed on the midrib of the pinnule (fig. 53b).

A reconstruction of *Eoangiopteris* is presented in text-fig. 2.

The linear, free-sporangiate sori of the genus *Grand'Eurya* Stur, from the Permo-Carboniferous of Autun, are quite similar to those of *Eoangiopteris*. In *Grand'Eurya*, however, there is no evidence of a receptacle, the sporangia being sessile on the pinnule. This difference presents a close parallel to the generic difference between *Scolecopteris* and *Asterotheca*.

Only two other linear marattiaceous fructifications are known which closely approximate *Eoangiopteris* in age. They are *Danaeites* Goeppert[16] from the European Coal Measures, and *Parapecopteris* Grand'Eury from the Upper Carboniferous of Gard and St. Étienne. However, their sporangia are laterally fused, while those of *Eoangiopteris* are entirely free from each other. Another major difference is the mode of attachment to the lamina; in *Eoangiopteris* the sori are elevated from the surface of the lamina by a receptacle, while, at least in *Danaeites*, they are sunken within the foliar tissue. These differences correspond closely in magnitude to the generic differences between the fructifications of such living marattiaceous genera as *Danaea* and *Angiopteris*.

A survey of the remaining known linear sori found among the fossils reveals none with which *Eoangiopteris* might be considered congeneric. A superficial examination of the Permian genus *Chansitheca* Rege (for a full account see Halle, 1927), which is known from compressions only, reveals a rather close similarity to *Eoangiopteris*, from the standpoint of general shape and distribution of the sori. *Chansitheca*, however, has sporangia with well-defined annuli, for which reason Halle ascribes to the genus a close affinity with *Oligocarpia* rather than with any marattiaceous entity.

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[16] The generic name implies a relationship with the modern genus *Danaea*. This implication has not met with credence, however, because of the lack of sufficiently detailed illustrations.

The Rhaetic genus *Marattiopsis* Schimper consists of linear fructifications, but here the alliance is obviously one with the modern *Marattia*, since the fructifications consist of two rows of fused sporangia, the whole structure opening much as the shell of a bivalve.

The upper Triassic fructification *Danaeopsis* Heer (also known only as compressions) consists not of fused sporangia, as might be inferred from the generic name, but of two rows of free sporangia extending from the margin to the midrib of the lamina. Discounting the great differences in size of the pinnules and numbers of sporangia in a single sorus, *Danaeopsis* resembles *Eoangiopteris* almost as closely as does the previously mentioned genus *Grand'Eurya*. The salient differences, however, are sufficiently obvious that confusion of the two genera is unlikely.

Among the living Marattiaceae with linear fructifications, the genera *Macroglossum*, *Archangiopteris*, and *Angiopteris* possess free sporangia, in which respect they resemble *Eoangiopteris*. While the fossil record is not yet sufficiently complete to allow us to draw incontestable conclusions as to phylogenetic series in the Marattiaceae, it seems reasonable to consider this fructification as an intermediate form between the Carboniferous radial sorus and the free-sporangiate linear sorus of today as typified by *Angiopteris*. For this reason the generic name *Eoangiopteris* is proposed. The generic and specific characters of *E. Andrewsii* are summarized in the following diagnoses:

Generic Diagnosis: Sori linear, consisting of several exannulate sporangia arranged in two opposed or slightly intercalated rows, and inserted by fleshy receptacles along lateral veins on dorsal surfaces of pecopterid pinnules; sporangia free from each other, with bases slightly sunken in receptacular tissue; dehiscence by longitudinal clefts along inner sporangial walls.

Specific Diagnosis: Pinnules measuring 7–9 × 2.50 to 3 mm., bearing 12 to 18 sori .90 to 1.35 mm. long, with 5 to 8 sporangia per sorus. Sporangia .75 to .90 mm. long, tapering from basal diameters of .20 to .30 mm. to bluntly acute apices; walls generally 2 cells thick. Spores round, with triradiate ridges and measuring 45–60 μ in diameter; exine with circular reticulations approximately 4 μ in diameter.

PHYLOGENETIC CONSIDERATIONS

I. THE PROBLEM: THE ORIGIN OF THE MARATTIACEAE

While the specimens described in the foregoing pages have added to the speciation of known fructification genera, to a clearer understanding of the nature of previously described species, and to the Carboniferous flora of the United States, their significance is not limited to those phases of paleobotany. It is the aim of paleobotany to fill in the numerous gaps in our understanding of plant evolution. The problem of the origin of the Marattiaceae has interested me for some few years, because they seem to have appeared upon the scene very suddenly during the Upper Carboniferous, leaving but few clues as to the nature of their pro-

genitors and the processes involved in their emergence as a well-defined and highly evolved fern group.

The problems of fern phylogeny are most successfully solved through comparative studies of the fructifications. Fortunately there was an amplitude of fructification specimens available for this investigation, and through their study several important points in connection with the phylogeny of the Marattiaceae have been brought to light.

II. THE "PHYLETIC SLIDE"

Studies of the various fern groups have shown that marginal or terminal fructifications are primitive, while those occupying a superficial position are advanced. The "phyletic slide," or migration of the sorus from the marginal to the superficial position, is a phenomenon which is known to occur independently in several groups of living ferns (see Bower, Vol. I, Chap. XII); it entails series of forms which display characters intergrading between the two extremes of soral position. While such series have greatly facilitated the understanding of family relationships, their presence has injected a great measure of difficulty into the task of drawing clear-cut lines of distinction between several of the families. In fact, the net result has been an extremely involved "phyletic bush" (see Bower, Vol. III, p. 2), containing intergrading and poorly defined families, with the Polypodiaceae (representing perhaps the epitome of polyphylesis and "indefinability" when considered as a single "family") occupying the most advanced position. This does not, of course, hold true for all the fern families, for at the base of the "bush", the eusporangiate families (Ophioglossaceae and Marattiaceae) present no difficulties when the "bush" as a whole is viewed. By virtue of their massive exannulate fructifications alone these two families occupy the two basal branches of the "bush"; furthermore, they are readily separable from each other by the position of the fructifications, those of the Ophioglossaceae occupying the primitive marginal position, and those of the Marattiaceae being borne superficially as clearly circumscribed sori, usually synangial. In succeeding pages an attempt will be made to explain the derivation of the superficial position of marattiaceous sori.

III. THE FOSSIL MARATTIACEAE

Marattiaceous fructifications are abundant in American coal balls from numerous localities. The lack of comprehensive and critical studies may be attributed to their small size, and it is very likely that many interesting specimens have been overlooked on this account.

Prior to the discovery of the pteridosperms, paleobotanists treated these fossils as archaic members of the Marattiaceae. Following this important discovery, however, the undeniable likenesses between the fossil and living fructifications came to be considered of less importance than the rather vague supposed likenesses between the marattiaceous fructifications and those presumed to be pteridospermous. Many attempts have been made to link these two unrelated groups upon

insufficient evidence. Kidston (1925) expressed this viewpoint in his exhaustive work on the British Carboniferous flora:

> In *Acitheca*, individual sporangia agree so closely with the microsporangia of *Telangium*, that the affinities of *Acitheca* seem to be Pteridospermous. If, then, this opinion as to the systematic position of *Acitheca* Schimper be correct, I do not see on what ground *Asterotheca* Presl and *Scolecopteris* Zenk. can be excluded from the Pteridosperms.
>
> It would therefore appear that the evidence in support of the occurrence of the Marattiaceous Ferns in Carboniferous times rests on supposition rather than on satisfactory proof. This statement may be thought too strong, but what has been learnt in regard to Pteridospermous microsporangia has undoubtedly weakened the grounds on which the belief in the existence of Carboniferous Marattiaceous Ferns was founded.

EVIDENCE RELATING TO THE MARATTIACEOUS AFFINITY OF THE FOSSIL FRUCTIFICATIONS

1. *A Comparison of Pteridospermous Microsporangiate Organs and Marattiaceous Fructifications.*—

All fructifications suspected of pteridospermous affinity resemble the marattiaceous fructifications *only* in their exannulate and sometimes synangial features (which are also found among the coenopterid fructifications, those of *Stauropteris* and *Chorionopteris* being exannulate, while those of *Corynepteris* and *Chorionopteris* are synangial). Other characters, however, if compared critically, seem to invalidate these similarities as grounds for seriously considering such forms as *Scolecopteris* and others as pteridospermous. These are:

a. Size and Complexity.—While the marattiaceous fructifications rarely attain lengths of more than two millimeters, the majority of the apparently pteridospermous male fructifications (*Dolerotheca, Potoniea, Whittleseya*, etc.) are huge in comparison; there is also a corresponding difference in spore sizes. Furthermore, the marattiaceous fructifications are structurally simple compared to the extremely complex organization of the fructifications mentioned above (see Halle, 1927; Schopf, 1948).

b. Manner in which the Fructifications are Borne.—In all instances where a closer compatibility of sizes can be demonstrated (*Telangium* and *Crossotheca*), the apparently pteridospermous fructifications are borne either terminally (this holds true for the larger forms, also) on naked frond ramifications or marginally on more or less peltate receptacles which terminate the ultimate frond divisions. All the known marattiaceous fructifications, however, are borne superficially on pinnules which show no difference from the sterile ones. *There is no known instance* of a pteridospermous microsporangiate fructification being borne superficially on monomorphic foliage.

c. Associations and Anatomical Evidence.—The following intimate fructification-foliage associations are known to occur: *Crossotheca* and *Sphenopteris* (Andrews and Mamay, 1948); *Goldenbergia* and *Neuropteris, Whittleseya* and *Alethopteris, Potoniea* and *Neuropteris* (Halle, 1929, 1933); *Dolerotheca* and *Alethopteris* (Schopf, 1948). There is good evidence for the pteridospermous affinity of the foliage genera mentioned above, and while association alone cannot always be held as conclusive evidence, Schopf (1948) has pointed out significant histological similarities between *Dolerotheca* fructifications and *Medullosa* stems

and petioles. On the other hand, *Pecopteris* foliage, upon which the marattiaceous fructifications are borne, is known to occur in intimate association with *Psaronius* stems. Furthermore, the u-shaped vascular strands of the pinnules upon which these fructifications are borne suggest them to be ultimate divisions of a stipitopterid psaronean petiole.

2. *A Comparison of Fructifications of the Living and Fossil Marattiaceae.*—

The following significant points of similarity are demonstrated by a comparison of the living and fossil members of this family:

a. There is a close similarity in sizes of the fossil and living fructifications and spores.

b. In both the living and fossil Marattiaceae, the fructifications are in the form of definitely circumscribed sori, either free-sporangiate or synangial, radial or linear. The similarities between *Ptychocarpus* (fossil) and *Christensenia* (living) and between *Eoangiopteris* (fossil) and *Angiopteris* (living) are much closer than any which can be demonstrated between the fossil marattiaceous sori and any supposedly pteridospermous fructifications.

c. In both the living and fossil Marattiaceae the sori are restricted to a superficial position, and the foliage is monomorphic (only in the living genus *Danaea* is there anything approaching the dimorphic condition).

d. *Psaronius* stems, which are frequently found in intimate association with fertile *Pecopteris* foliage, show a close anatomical similarity to the living marattiaceous genus *Angiopteris*, and cannot be confused with any known pteridospermous stem. Furthermore, the u-shaped trace of the psaronean petiole *Stipitopteris* is quite similar to the traces found in fertile pecopterid pinnules.

It is my opinion that the foregoing evidence, if carefully considered, should lead to the conclusion that the existence of a well-defined group in the Paleozoic, corresponding in a remarkable fashion to the living Marattiaceae, cannot be reasonably denied. Furthermore, efforts made in respect to this group should be directed toward the solution of problems bearing upon their poorly understood phylogeny rather than attempting to correlate them with the pteridosperms on slender threads of evidence.

IV. A PROPOSED EXPLANATION OF THE ORIGIN OF THE MARATTIACEAE

The following facts with reference to the fossil Marattiaceae become increasingly important:

1. The fossil fructifications are essentially identical with the living ones; evolution of the fructifications had apparently reached its peak during late Paleozoic times and then leveled off.

2. The superficial position of the sorus, considered to be the climactic evolutionary result, had been well established in the Marattiaceae by Upper Carboniferous times.

Tentatively accepting the Marattiaceae as derivatives of some branch of the coenopterids, it seems likely that various stages in the migration of the sorus to

the superficial position might be sought in the coal balls, since the two groups were contemporaneous during at least part of their respective geological histories, and fructifications of both groups are frequently found within the same petrifaction. In searching for intermediate forms, then, we would look for either coenopterid fructifications showing tendencies toward the marattiaceous types (massive sporangial walls, synangia, or otherwise closely circumscribed sori) and occupying a terminal or marginal position, or for marattiaceous fructifications occupying marginal or only slightly superficial positions on the lamina.

A. A Review of Coenopterid Soral Morphology

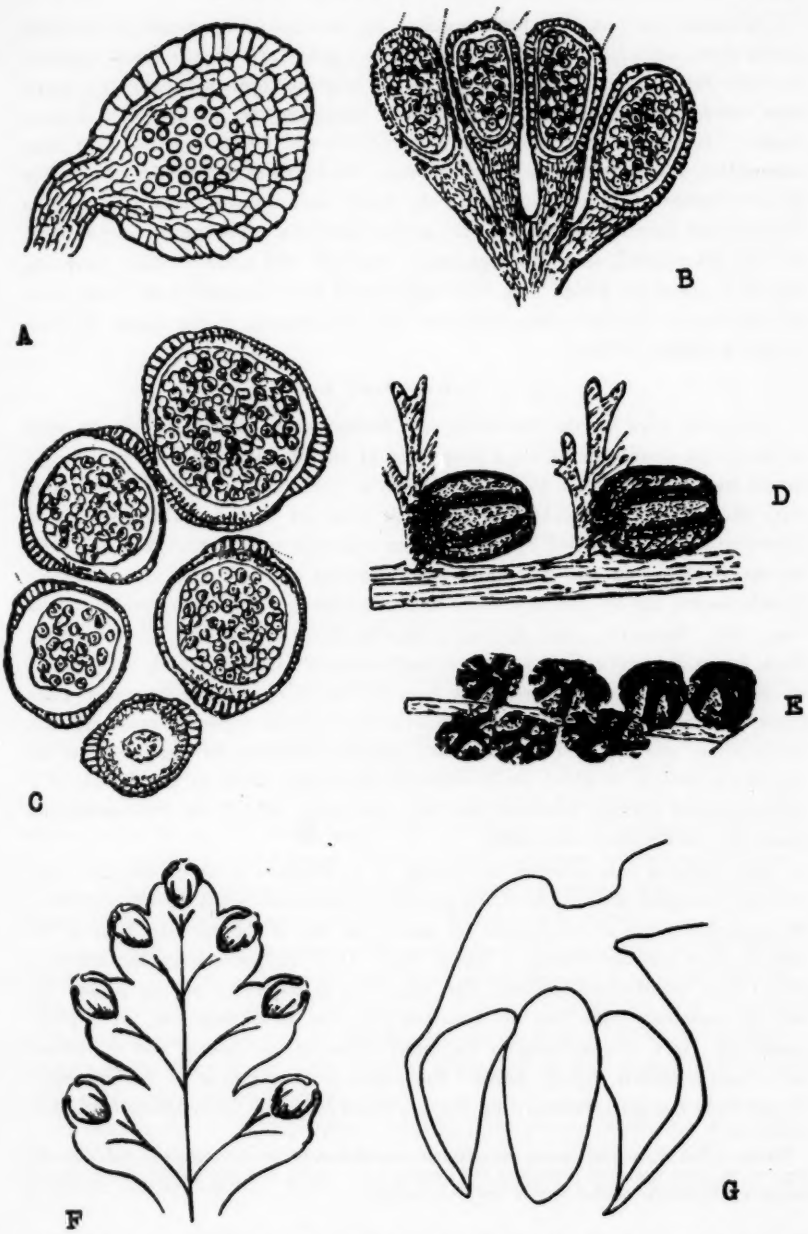
In the following brief review of the outstanding aspects of some of the known coenopterid fructifications, we shall follow the sequence which Bower (Vol. II, p. 39) suggests to represent a line of soral evolution among the coenopterids.

Beginning with the simplest type of fructification, that of *Stauropteris* (see text-fig. 3A), we see that the sporangia are massive-walled, exannulate structures which are borne singly, each occupying the terminal position upon an ultimate ramification of the plant, much in the same manner as the sporangia of *Rhynia*. Continuing with the series, the sporangia of the fructification *Etapteris* (*B* and *C*) appear singly in the terminal position, but are arranged into rather lax tassel-like groups, each group suggesting a derivation from a *Stauropteris*-like progenitor by the aggregation of several individual sporangia. Although this concept is somewhat confused by the appearance of a rather well-developed annulus in *Etapteris*, the chief significance lies in the apparent tendency of the sporangia to become condensed into more intimate association with each other. A further continuation of this tendency may be seen in the genus *Corynepteris* (*D* and *E*), in which the sporangia possess annuli much like those of *Etapteris*. However, the condensation of the sporangia has been furthered to the extent that well-defined sori are present in which the sporangia are closely appressed. The sori are borne upon the margins of narrow pinnules. This is the first appearance of a lamina in this series.

The culmination of the tendencies shown in this series appears in the fructification *Chorionopteris* (*F* and *G*). Although this fructification has been reported but once, enough is known of its structure to afford the following significant facts:

1. The fructifications are massive-walled synangial groups of four sporangia each, with a continuous sheath surrounding the entire structure.

2. The fructifications are borne singly at the terminations of the lateral veins of a narrow, fleshy pinnule; the pedicels and synangial walls were originally described as "continuations of the tissues of the lateral veins." The synangia are seen to extend from the tips of the foliar lobes; they may thus be termed either *marginal* or *terminal*, depending upon whether the reference is made to the lamina or veins.



Text-fig. 3. *A*, *Stauropteris Oldhamia* Binney, from Bower, after Mrs. D. H. Scott (approx. × 50); *B*, *C*, *Etapteris* sp., from Bower, after Renault (*B*, approx. × 10, *C*, approx. × 20); *D*, *Corynepteris Essenghi* Andrae, from Bower, after Zeiller (approx. × 10); *E*, *Corynepteris coralloides* Gutbier, from Bower, after Zeiller (approx. × 5); *F*, *G*, *Chorionopteris gleichenioides* Corda, from Hirmer, after Kubart (*F*, approx. × 9, *G*, approx. × 20).

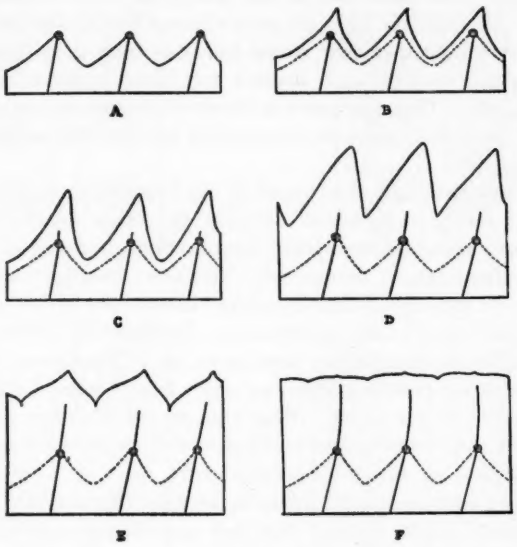
Although the fact that both annulate and exannulate sporangia are involved in the above series seems to cast doubt upon its validity as a single natural sequence, its value lies in the apparent tendency of the fructifications to become aggregated into compact groups which are ultimately borne on the margin of a distinct lamina. It appears that the genera *Stauropteris* and *Chorionopteris*, with their exannulate, thick-walled sporangia, represent the opposite extremities of one line of development within the coenopterids, which leads to the Marattiaceae. The intermediate members of this line are as yet unknown. The genus *Corynepteris*, on the other hand, seems to represent a stage in still another series involving annulate sporangia, which may have culminated in a gleicheniaceous form such as *Oligocarpia*. Information concerning the development of the lamina in these genera is totally lacking.

B. A "Phyletic Slide" Series

Referring back to the fructification *Chorionopteris*, its salient features seem to fulfill the qualifications for a progenitor of the Marattiaceae.[17] The synangia would be easily confused with a scolecopterid fructification if their relationship with the coenopterid petiole *Anachoropteris* were not known. The sporangia of *Chorionopteris* are enclosed by a continuous synangial wall, a feature which is by no means absent in the pecopterid fructifications. It is found in the genera *Cyathotrachus* and *Ptychocarpus*, and in young synangia of *Scolecopteris incisifolia* (fig. 34). Since the chief difference between *Scolecopteris* and *Chorionopteris*, then, lies in their relative positions on the lamina, we are faced with the problem of demonstrating stages intermediate between the marginal and superficial positions. The species *Scolecopteris incisifolia* and *S. latifolia* appear to represent such intermediate stages; the evidence points toward migration of the sorus to the superficial position in which *proliferation* of the upper tissues of the margin of a chorionopterid pinnule produced one like that upon which the two mentioned species of *Scolecopteris* were borne.

The reader is now referred to text-fig. 4, in which a series of diagrams representing marginal portions of fertile pinnules is presented. In *A (Chorionopteris)*, the synangial points of attachment are seen at the tips of the marginal lobes of the pinnule, each one terminating a lateral vein. In *B* (hypothetical) the marginal tissues have proliferated slightly; the inter-lobal embayments of the lamina are still comparatively wide; but the synangial points of attachment are now slightly superficial. In *C* (hypothetical), the proliferation has continued, and the lateral veins have extended slightly beyond the points of attachment of the synangia. *D* represents a stage approximating the condition found in *Scolecopteris incisifolia*

[17] Bower (Vol. II, p. 39) states, in reference to *Chorionopteris*: "A 'phyletic slide' of the sorus to the lower surface of a widening leaf segment . . . . would then give a soral state similar in structure and position to that seen in the Marattiaceae."



Text-fig. 4. Illustrating a possible "phyletic slide" series, beginning with the coenopterid fructification *Chorionopteris* and resulting in the marattiaceous fructification *Scolecopteris*. Shaded circles represent the points of insertion of the synangia; broken lines the original foliar margin shown in *A*.

(compare with text-fig. 1) and *Scolecopteris latifolia*. The lobes are now proportionately longer than wide, and the embayments of the lamina are quite narrow. The synangia are inserted near the bases of the marginal lobes and the ends of the lateral veins, and are now quite superficial in position. In *E* (hypothetical) the lobes have undergone lateral fusion to some extent, a process which is culminated in *F*, in which the margin of the pinnule is essentially entire. This would correspond to the condition seen in *Scolecopteris iowensis* or *S. minor*.

Such a series may also be seen in the ontogeny of various genera of the living Schizaeaceae. The young sporangia begin their development in a marginal position, to be followed by a proliferation of the upper tissues of the margin of the lamina, causing the matured sporangia to assume a superficial aspect. This may represent the ontogenetic reflection of a phylogenetic series such as diagrammed in text-fig. 4, but involving annulate sporangia.

As seen in fig. 17 *(Scolecopteris latifolia)*, the tissues composing the long, narrow marginal lobes seem quite definitely to be direct continuations of the upper epidermal and hypodermal tissues which are characterized by their dense black

cellular contents. This aspect may be best seen in fig. 22, a transverse section of a single lobe. Although the lobes are quite discrete bodies, they are very closely crowded, and it appears that their lateral fusion to form a continuous-margined lamina such as that upon which S. *iowensis* was borne, would present little evolutionary difficulty. Thus the genus *Scolecopteris* is seen to contain forms (S. *latifolia* and S. *incisifolia*) which are intermediate between the marginal and superficial conditions.

There yet remains one puzzling aspect of this hypothesis. Among the coenopterid fragments present in American coal balls, the petiole *Anachoropteris*, which is known to have borne *Chorionopteris* fructifications, is found in numbers exceeded only by fragments of *Botryopteris*. However, fructifications which compare in detail with the original descriptions and illustrations of *Chorionopteris* still remain to be discovered in our petrifactions. Furthermore, although the stems upon which *Anachoropteris* petioles were borne are still unknown, the comparatively large size of the petioles suggests an origin from a stem of such magnitude that it could hardly escape notice. What then are we to deduce from the total absence of stems and fructifications in floras so rich in petiolar fragments? The following suggestions are offered for consideration:

1. The close fundamental resemblances between *Chorionopteris* and various of the scolecopterid species suggests that they compose an evolutionary complex of intergrading forms, and any or all of the intermediate forms presented in the series shown in text-fig. 4 might be sought within either genus. The generic distinction would then depend upon the vascular anatomy of the supporting petiole.

2. *Anachoropteris* petioles, when seen in transverse section, display vascular strands with similar structure to those of the psaronean petiole *Stipitopteris*, with the exception of the position of the protoxylems. They may in all likelihood be ultimately proven to be borne on *Psaronius* stems or upon stems of intermediate structure between *Psaronius* and certain coenopterid stems.[18]

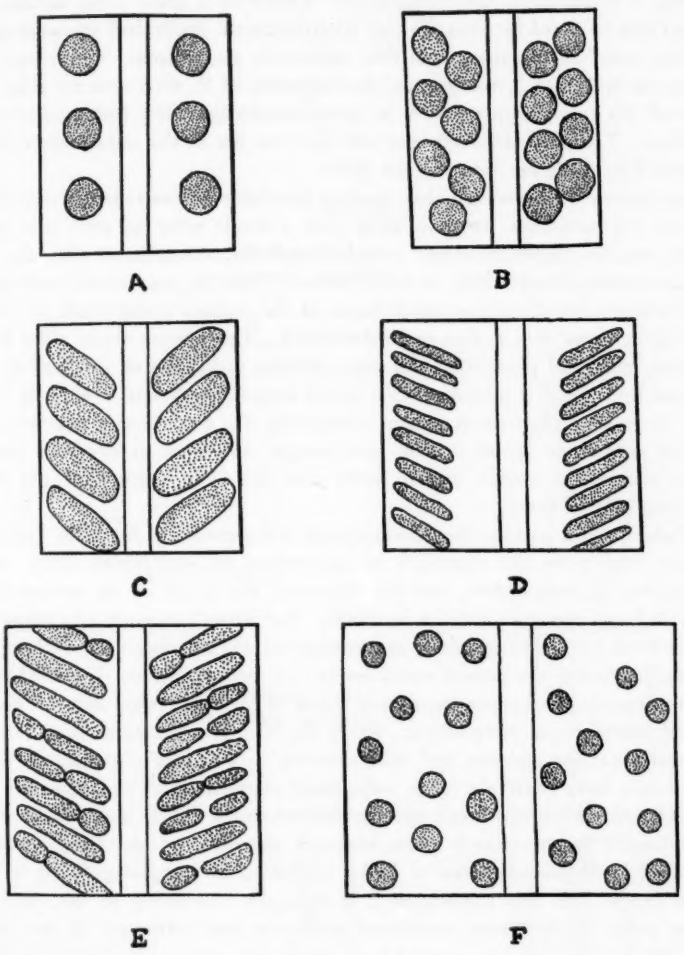
While the hazards of basing conclusions on the association of plant fragments are fully realized the bulk of the evidence uncovered to date strongly indicates a derivation of the fossil Marattiaceae from the anachoropterid coenopterids, involving the migration of the sori from the marginal to the superficial position, as diagrammed in text-fig. 4.

V. EVOLUTIONARY POSSIBILITIES AMONG THE MARATTIACEAE

A. THE DERIVATION OF LINEAR SORI

Upon the basis of the evidence uncovered during this work, we shall now consider the evolutionary possibilities within the Marattiaceae. One of the chief remaining problems lies in the derivation of the linear sorus, now predominant among the living Marattiaceae. Referring back to the description of *Scolecopteris*

[18] Lenz (1942) wrote: "This paper is intended as a further contribution to the apparent relationship between petioles described as *Anachoropteris* and *Stipitopteris* and fern stems described as *Psaronius* and *Caulopteris*."



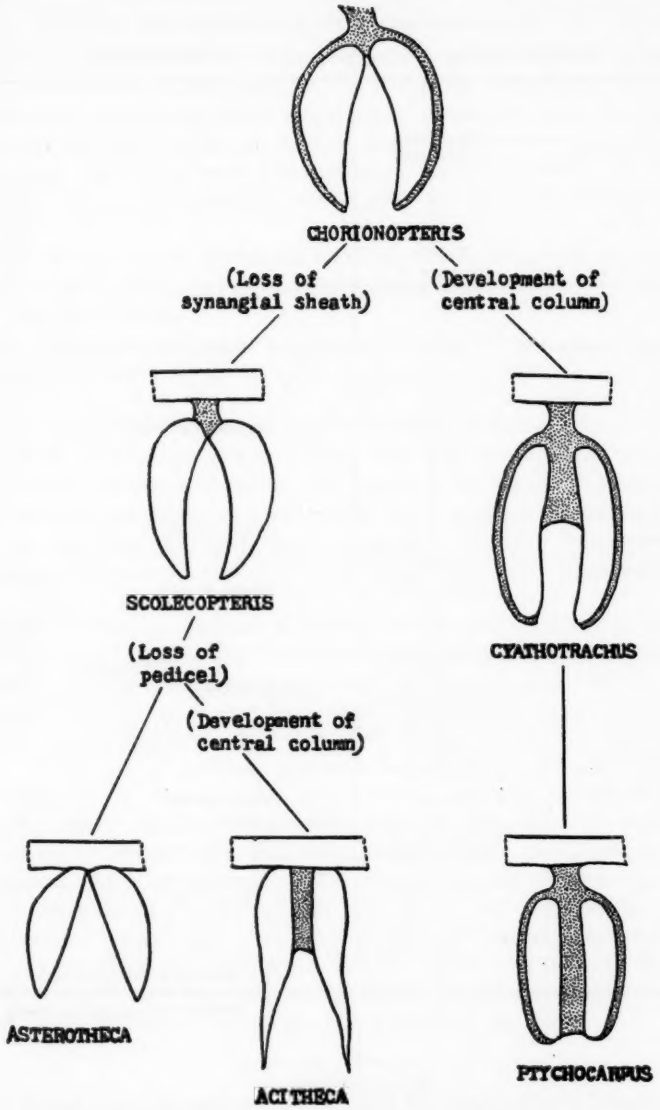
Text-fig. 5. Illustrating a possible sequence in the evolution of marattiaceous fungi: *A*, a typical asterothecous fructification, with the usual uniseriate condition; *B*, in which *two* rows of sori are borne on each side of the midrib, (sometimes seen in *Scolecopteris iowensis*); *C*, linear sorus such as in *Eoangiopteris* resulting from fusion of crowded radial sori such as shown in *B*. Expansion of the lamina might produce either of the two conditions: *D*, in which the sori are situated near the margins and away from the midrib (as in *Angiopteris*); or *E*, partial fission of the linear sori (sometimes seen in *Danaea*). Further expansion and fission might result in irregularly distributed radial sori as seen in *Christensenia (F)*.

iowensis, a radial sorus, and *Eoangiopteris Andrewsii*, a linear sorus, certain similarities may be noted between the two fructifications. Individual sporangia of the two are similar in size, shape, and their dehiscence mechanisms. The tissues comprising the pedicel of S. *iowensis* and the receptacle of *E. Andrewsii* are alike. The spores of the two compare closely in gross morphology, size, and sculpturing of the exine. The chief difference between the two lies in the radial aspect of one as opposed to the linear aspect of the other.

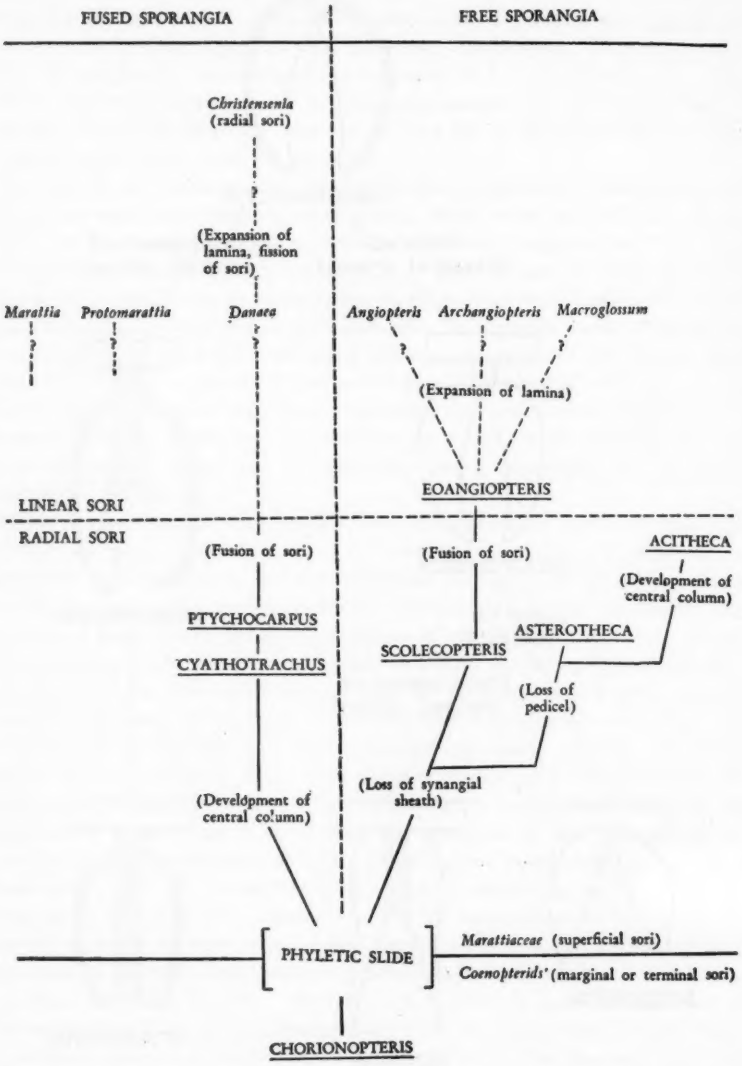
One feature of S. *iowensis* that deserves particular comment is that the fructifications are sometimes borne in *more than a single series* on each side of the midrib, resulting in an extremely crowded condition, as compared with the usual uniseriate arrangement found in other species. This suggests an ultimate *fusion* of sori along a lateral vein; eventual fusion of the pedicels would result in a linear, receptacular sorus such as that of *E. Andrewsii*. This process would allow for an increased sporangial production and more efficient utilization of the limited space provided by as small a pinnule as that which bore *E. Andrewsii*. While it is difficult to make a concrete statement concerning the evolutionary position of S. *iowensis* within the genus, its low spore output points to an advanced position among the known species, and it seems that this is in support of the *fusion* hypothesis offered above.

While it seems possible that *Eoangiopteris* was derived by *fusion* of radial sori and may have given rise eventually to the modern free-sporangiate linear sori of *Angiopteris*, *Archangiopteris*, and *Macroglossum*, the origin of the modern linear sori with fused sporangia remains in doubt. Conceivably the sori of *Danaea* may have evolved by a similar fusion of synangia of the *Ptychocarpus* type; an accompanying loss of the pedicel would result in a sorus similar to that of *Danaea*.

An interesting circumstance is to be noted in the relationship between pinnule size and fructification morphology. While the fossil fructifications were borne on very small, narrow pinnules and were crowded very closely together, the living Marattiaceae have relatively large, wide foliar segments with numerous but uncrowded sori. While the fossil sori are predominantly radial, the living ones are predominantly linear; thus it seems that the expansion of the lamina was accompanied by the development of linear fructification morphology, that is, *to a certain extent*. In this connection it is especially interesting to note that the modern genus *Christensenia*, considered to be the most advanced of the Marattiaceae by virtue of its dorsi-ventral habit, small size, large scales, highly expanded foliar segments and reticulate venation, produces *radial sori* which are very similar to the fossil sorus *Ptychocarpus*. Bower (1923) contends that the radial sori of *Christensenia* have been derived through the fission of a linear sorus of the *Danaea* type, accompanying an expansion of the lamina. Thus, if the proposed hypothesis of *soral fusion* may be considered a reasonable one, it appears that evolution of the marattiaceous sorus has undergone a complete reversal, with the archaic progenitors and most recent derivatives displaying essentially the same sort of soral morphology. This evolutionary sequence is diagrammed in text-fig. 5.



Text-fig. 6. Showing two possible lines of derivation of asterotheceous fructifications. Beginning with the coenopterid fructification *Chorionopteris*, the line of development shown at the right involves development of a central column and results in asterothecous sori with *fused* sporangia. The line of development shown at the left involving loss of the synangial sheath, loss of the pedicel, and development of a central column, results in asterothecous sori with *free* sporangia.



Text-fig. 7. A proposed phyletic chart of the Marattiaceae.

B. The Derivation of the Various Radial Sori

Returning to the fructification *Chorionopteris*, it appears that as a progenitor for the asterotheceous fructifications, only a few minor evolutionary alterations are necessary to produce the latter several types. These fall into two distinct lines (see text-fig. 6).[19] Although *A*, *B*, *C*, and *D* involve free-sporangiate sori, while *E* and *F* represent sori with fused sporangia, a complete series such as illustrated might have been accomplished within either the fused- or free-sporangiate soral groups.

1. By retention of the pedicel and synangial sheath, along with the development of a central column, the *Ptychocarpus* type might be produced, with *Cyathotrachus* as an intermediate.

2. By reduction of the synangial sheath, the *Scolecopteris* and *Asterotheca* types might be derived, depending upon the simultaneous retention or reduction of the pedicel. By the development of a central column in a fructification of the *Asterotheca* type, an *Acitheca*-like fructification might be derived.

The above evolutionary processes, along with that presented in text-fig. 4, would result in the above-mentioned soral types, in the superficial position. It thus appears that pedicellate sori with fused sporangia represent the most primitive type, with sessile, free-sporangiate forms advanced. (This is in direct opposition to the series proposed by Graham (1934), in which sessile forms are considered to be primitive.)

The Marattiaceae are proposed as having been derived from the coenopterid ferns, involving a "phyletic slide" in which the coenopterid genus *Chorionopteris* is the primitive form (text-fig. 4). The superficial marattiaceous sori appear to have developed along two distinct lines: those with fused sporangia placed at the left of the vertical broken line, and those with free sporangia at the right (text-fig. 6). Within each of these two groups are found both the primitive *radial* sori (placed below the horizontal broken line) and the apparently derived *linear* sori (above that line). Although *Christensenia* produces radial sori, it is apparently the most highly evolved form and consequently occupies the highest position among genera with fused sporangia. All fossil genera are underlined in this chart. While future work in the field of coal ball research will undoubtedly modify the phylogenetic trends suggested in the foregoing pages and diagrammed in text-fig. 7, such discoveries are eagerly awaited by the author with the hope that they will greatly amplify our knowledge of the past history of this interesting group of ferns. Any criticisms or suggestions will be gratefully accepted.

Acknowledgment

The author wishes to express appreciation of the many valuable suggestions of Dr. Henry N. Andrews, under whose direction the present work was accomplished. Thanks are also due the Director of the Missouri Botanical Garden for making

[19] Because of its apical annulus, the genus *Sturiella* is of doubtful affinity and is not considered here.

available the library facilities, and Dr. Rolla Tryon, for offering constructive suggestions during the course of this work.

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EXPLANATION OF PLATE

PLATE 1

Figs. 1–4. *Botryopteris fecunda*

Fig. 1. A group of three sporangia, sectioned longitudinally. The pedicel of the sporangium at the left may be seen at the top of the figure. Slide #1680, × 100.

Fig. 2. Two sporangia, sectioned transversely. Note the annulus-like differential thickening of the sporangial walls. Slide #1680, × 120.

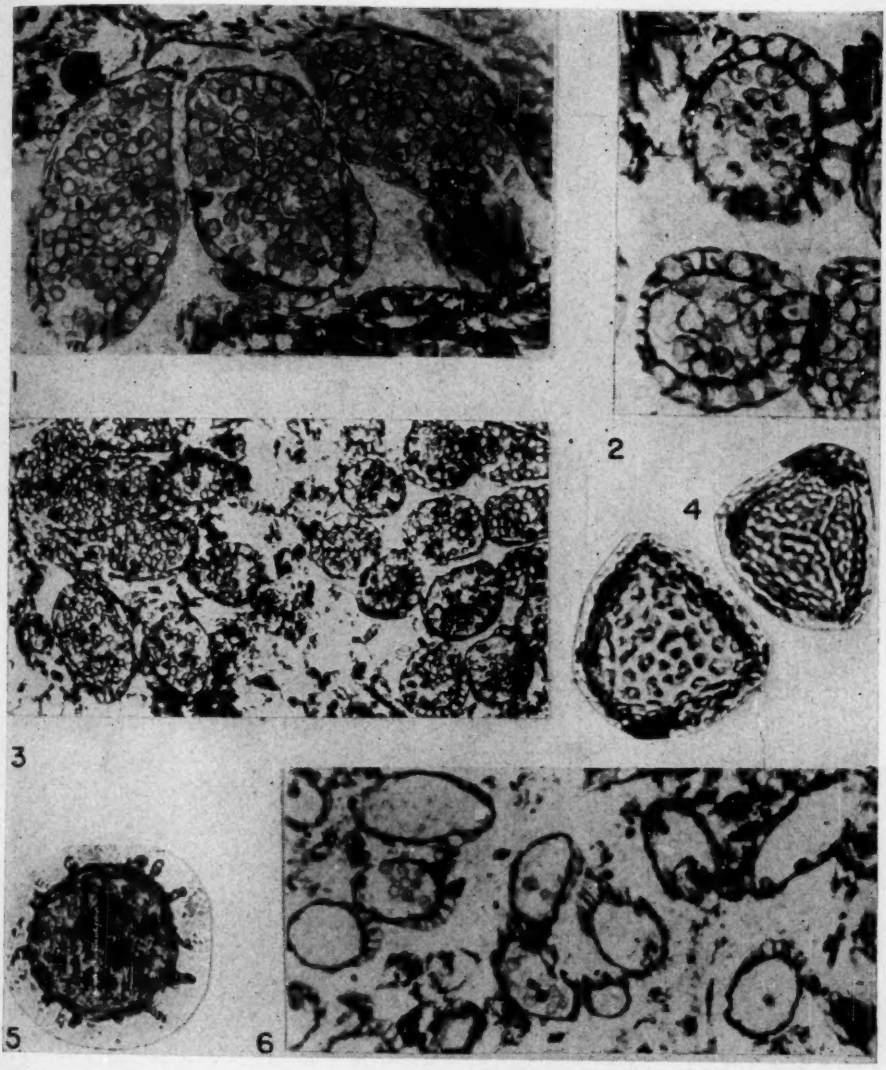
Fig. 3. A group of closely crowded sporangia, sectioned both transversely and longitudinally. Slide #1680, × 53.

Fig. 4. Spores. Note the tetrahedral shape and triradiate ridge. Slide #1680, × 700.

Figs. 5, 6. *Botryopteris spinosa*

Fig. 5. Spore. Note the blunt spine-like projections. Slide #1683, × 500.

Fig. 6. A group of loosely aggregated sporangia, sectioned both transversely and longitudinally. Slide #1683, × 45.



MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 2

Figs. 7, 8. *Botryopteris spinosa*

Fig. 7. A group of sporangia, the largest one sectioned longitudinally. Note the short pedicel at the upper right. Slide #1683, × 135.

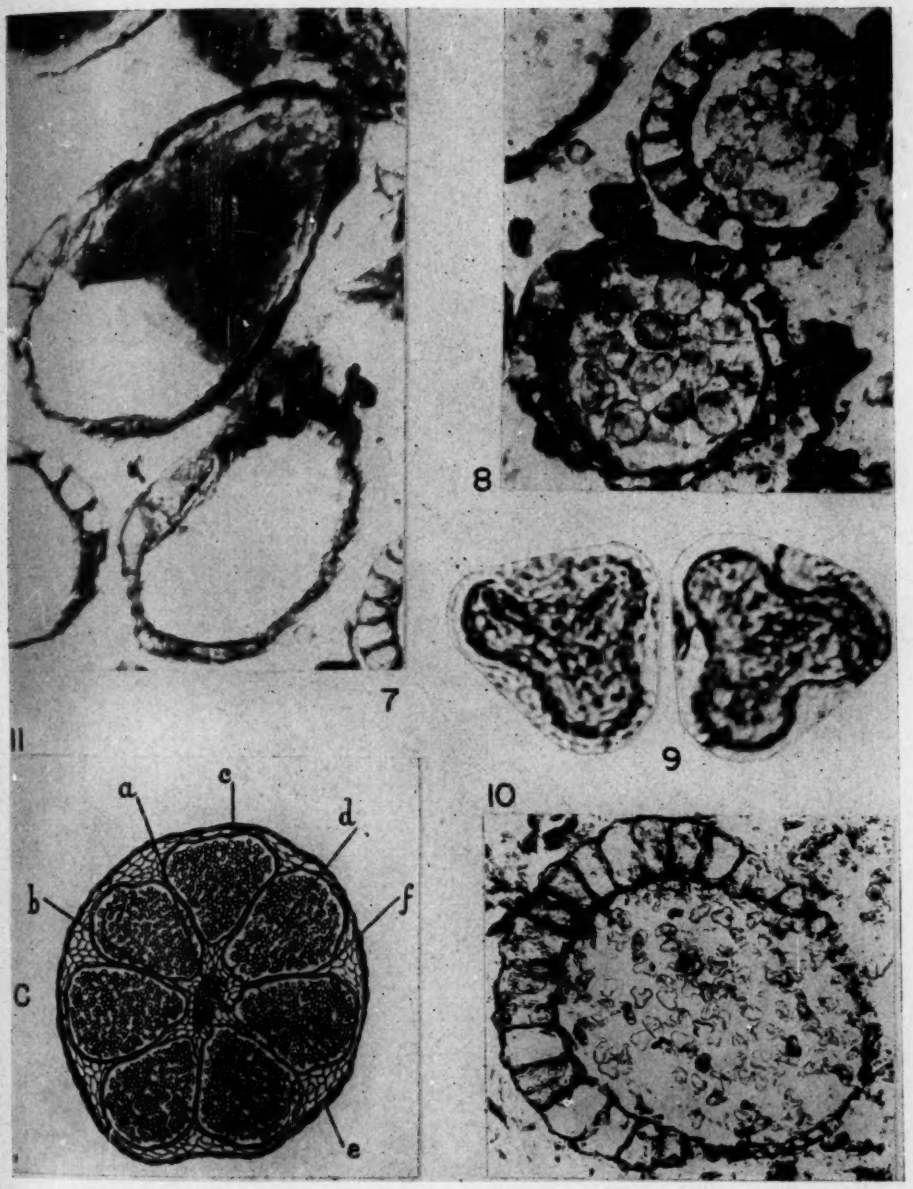
Fig. 8. Two sporangia, sectioned transversely. Note the thin sporangial walls, with annulus-like thickenings. Slide #1683, × 155.

Figs. 9, 10. *Botryopteris illinoensis*

Fig. 9. Spores. Slide #1685, × 1360.

Fig. 10. A single sporangium, sectioned transversely. Note the markedly differential thickening of the sporangial wall, which is a single cell in thickness. Slide #1686, × 165.

Fig. 11. *Ptychocarpus unitus* Brongniart. A single synangium, sectioned transversely. *a*, bundle of receptacle; *b*, its parenchyma; *c*, tapetun; *d*, spores; *e*, *f*, common envelope of synangium. Figure and explanation from Bower, after Renault, ×60.



MAMAY—FERN FRUCTIFICATIONS

Explanation of Plate

PLATE 3

Cyathotrachus altissimus

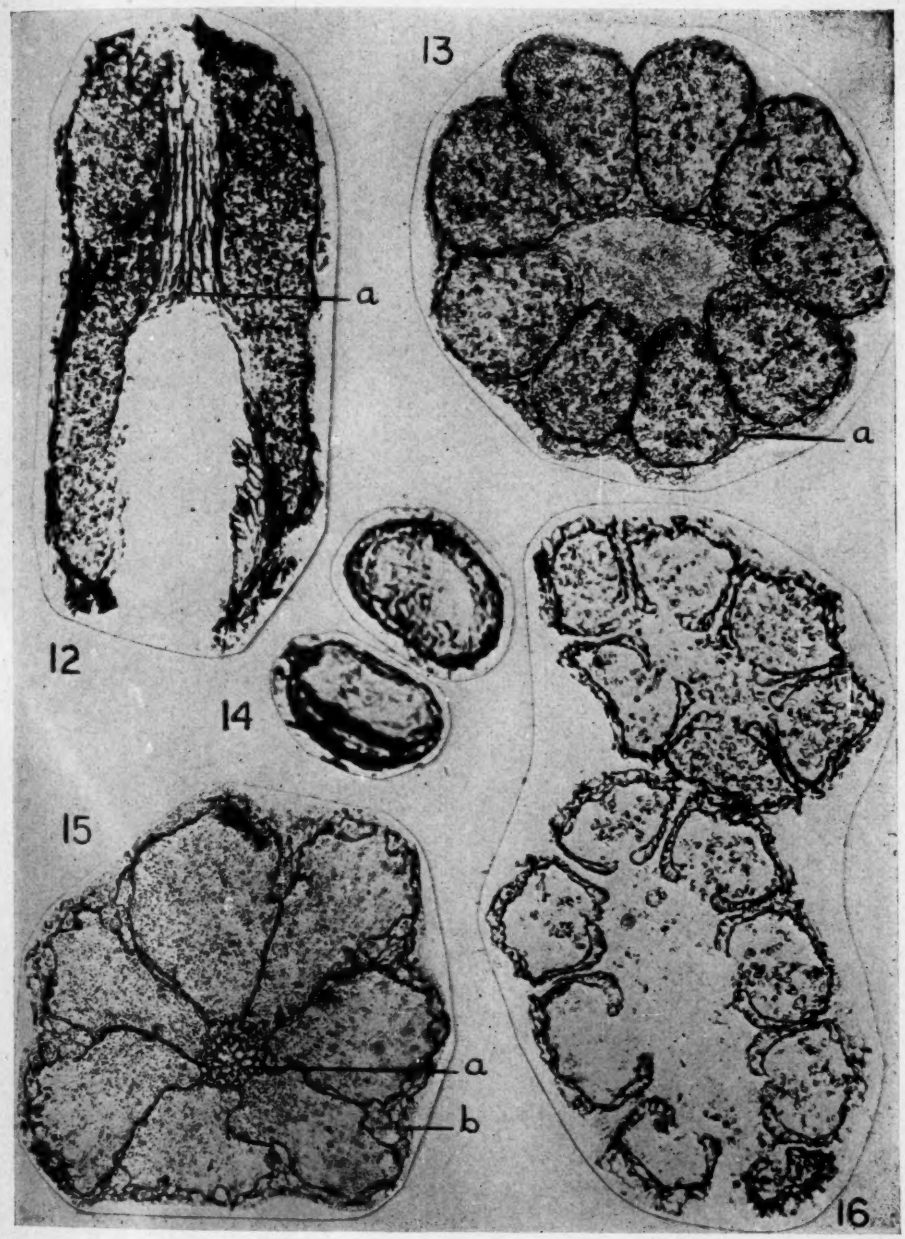
Fig. 12. A single synangium, sectioned longitudinally. Note the hollow cup-like portion of the fructification, extending distally from the termination of the central column (*a*). Slide #1687, × 50.

Fig. 13. A single synangium, sectioned transversely through its hollow cup-like portion, with spore masses intact. *a*, continuous synangial wall (compare with *e*, *f*, fig. 11). Slide #1692, × 60.

Fig. 14. Spores. Slide #1688, × 1300.

Fig. 15. A single synangium, sectioned transversely through the central column. *a*, central column; *b*, synangial wall. Slide #1688, × 60.

Fig. 16. Two dehiscent synangia, sectioned transversely. Note that the sporangia have separated from each other and display slits of dehiscence at their innermost surfaces. Slide #1688, × 70.



MAMAY—FERN FRUCTIFICATIONS

Explanation of Plate

PLATE 4

Scolecopteris latifolia

Fig. 17. Two pinnules, transversely sectioned, with attached synangia. Note the broad, strongly inflexed margins of the pinnules. Slide #1697, × 15.

Fig. 18. A pinnule sectioned parallel to the plane of the lamina, with several synangia shown sectioned transversely. Note the predominance of trilocular synangia, and the dense black contents of the cells of the epidermis and hypodermis (*a*). Slide #1694, × 18.

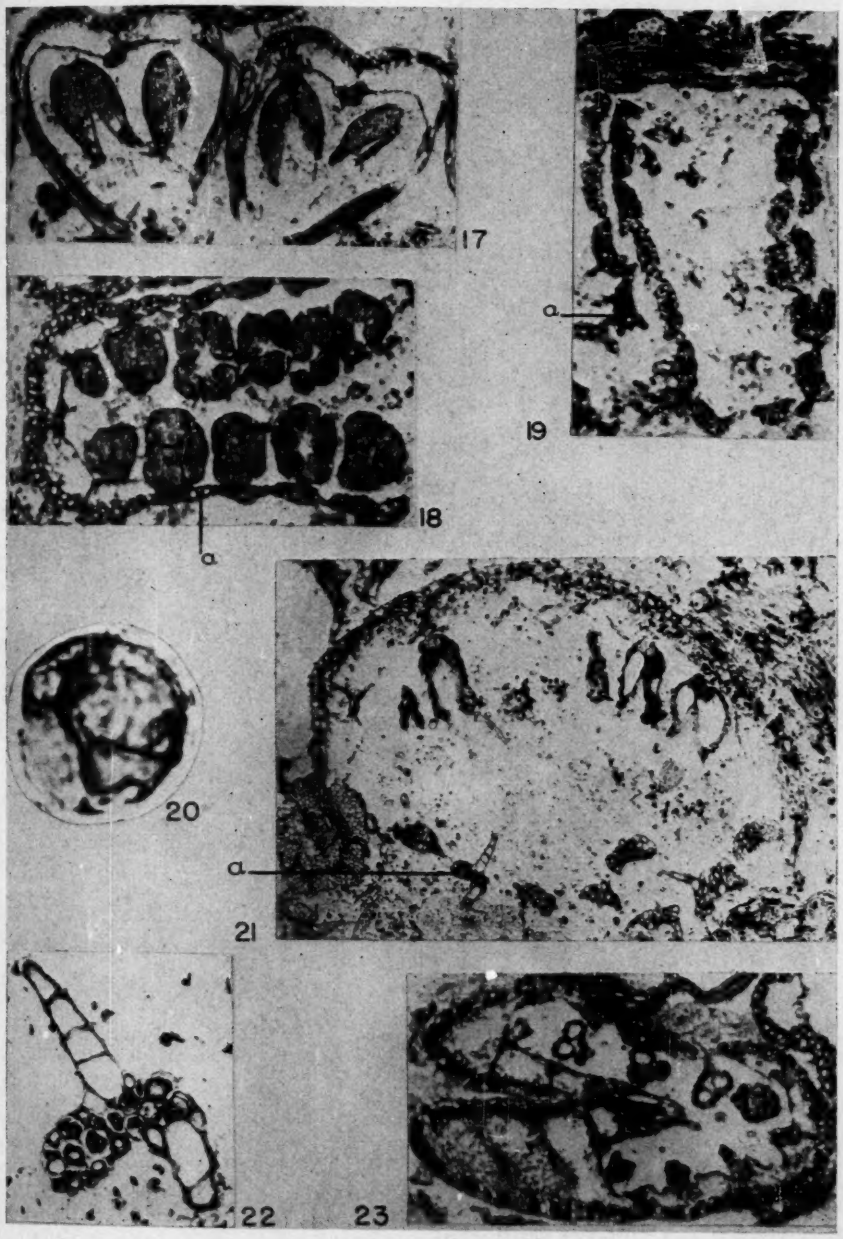
Fig. 19. A single pinnule and portions of the margins of two adjacent ones, sectioned in a plane paralleling that of the lamina, but below the apices of the fructifications. The penultimate midrib is shown at the upper portion of the figure. Note that the inflexed pinnule margins are dissected, appearing as series of separate crescent-shaped bodies with dense cellular contents. *a*, a single lobe of the pinnule margin. Slide #1694, × 16.

Fig. 20. Spore. Slide #1697, × 800.

Fig. 21. A single pinnule, sectioned in a plane parallel to its midrib, but near one "shoulder" of the pinnule, with the section intercepting several of the attached synangia. The penultimate midrib is shown at the left, transversely sectioned. At the bottom of the figure are shown transverse sections of the strongly inflexed marginal lobes, one of which is indicated at point *a*. Slide #1696, × 17.

Fig. 22. Higher magnification of the lobe seen in figure 21, *a*. Note the epidermal hairs and the dense cellular contents. Slide #1696, × 70.

Fig. 23. A single pinnule, sectioned parallel to the plane of the lamina. A portion of the midrib and several of the lateral veins are shown, along with several synangia, sectioned transversely near their bases. The hypodermis appears as a nearly continuous black outline to the pinnule. Slide #1694, × 17.



MAMAY—FERN FRUCTIFICATIONS

Explanation of Plate

PLATE 5

Scolecopteris iowensis

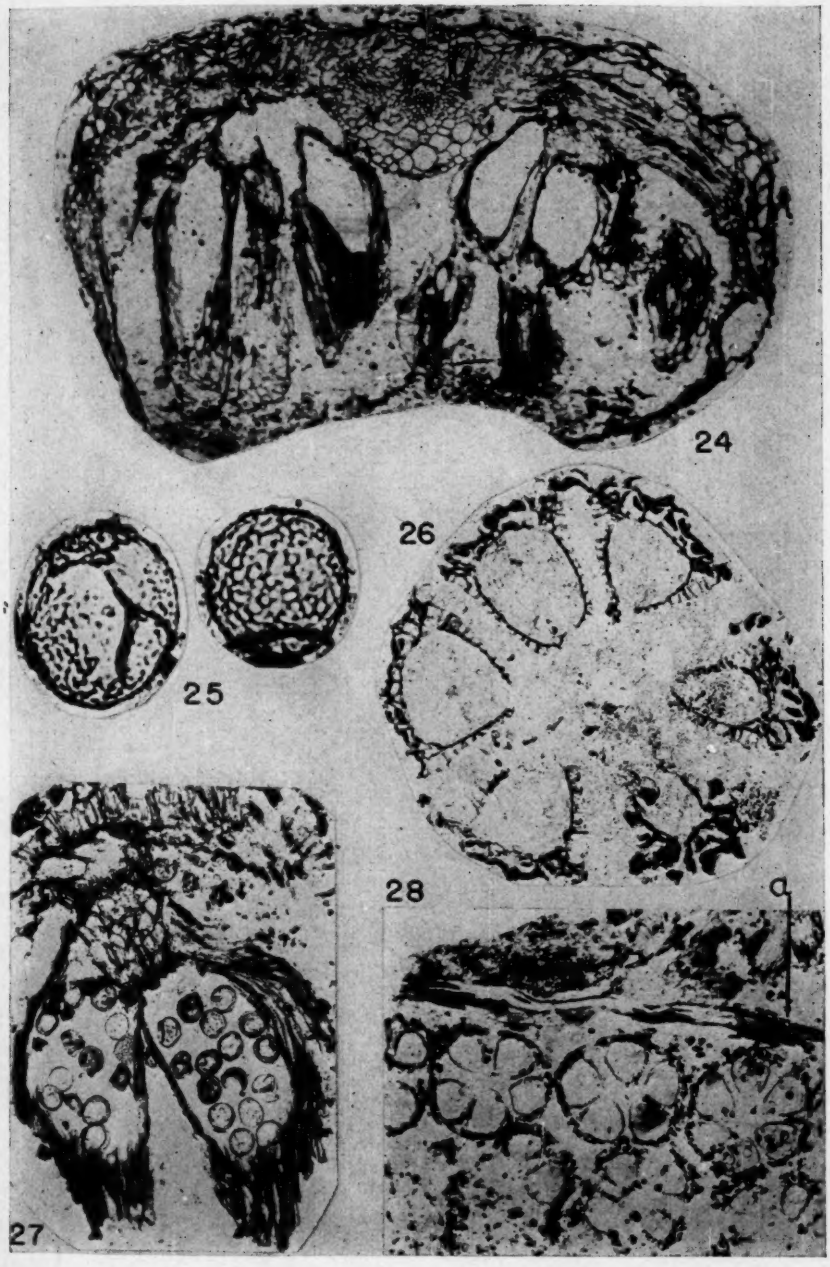
Fig. 24. Transverse section of a pinnule, with fructifications attached. Note the strong midrib and inflexed pinnule margins. Slide #1698, × 36.

Fig. 25. Spores. Note the reticulate exines and triradiate ridge. Slide #1702, × 350.

Fig. 26. Transverse section of a synangium containing six sporangia. Note the dense cellular contents of the outer walls, and the thin inner sporangial walls. Slits of dehiscence are evident at the innermost portion of each sporangial wall. Slide #1702, × 74.

Fig. 27. Longitudinal section of a synangium, showing its pedicellate attachment to the pinnule. Slide #1698, × 60.

Fig. 28. Portion of a pinnule, sectioned in a plane paralleling the lamina. At one side of the midrib (*a*) are shown two closely appressed rows of synangia. Slide #1702, × 20.



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Explanation of Plate

PLATE 6

Scolecopteris minor Hoskins var. *parvifolia* Mamay

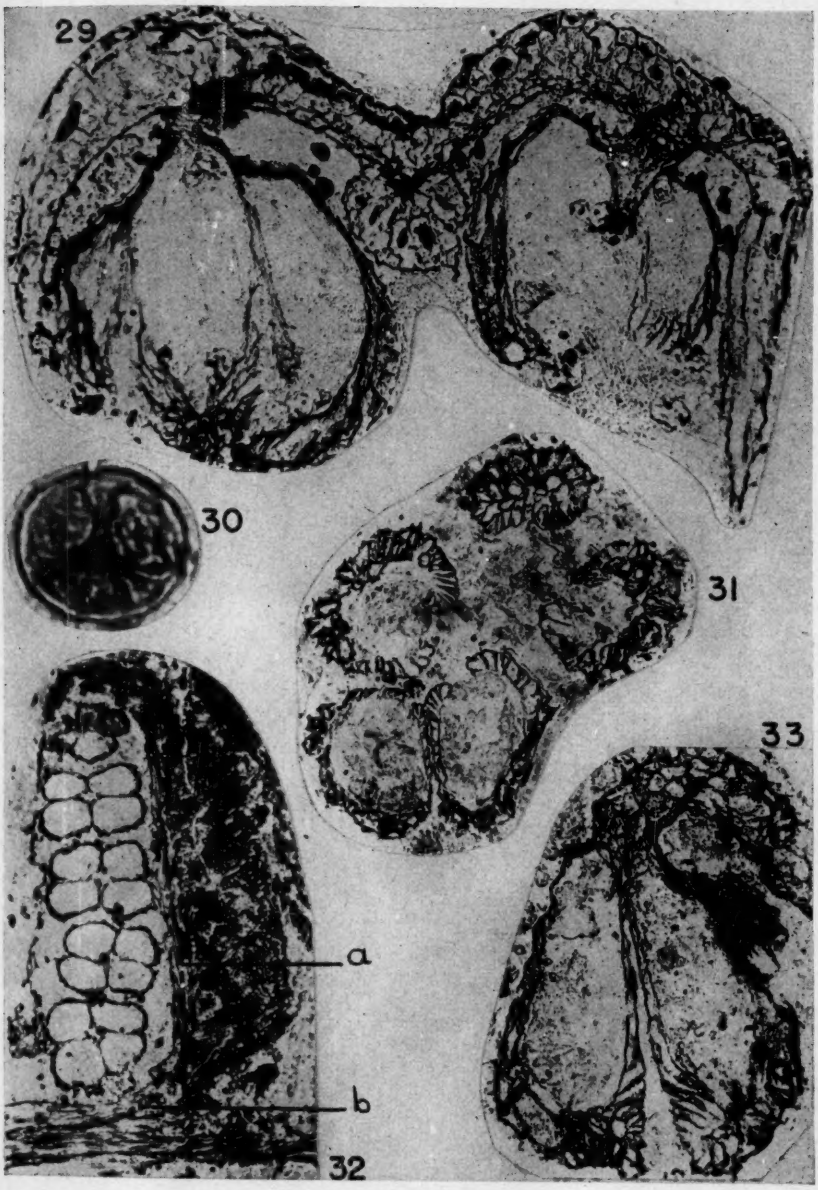
Fig. 29. Transverse section of a pinnule with two synangia attached. Note the strong midrib and inflexed pinnule margins. Slide #1704, × 66.

Fig. 30. Spore. Note the triradiate ridge. Slide #1703, × 1650.

Fig. 31. Transverse section of a synangium containing five sporangia. Slide #1708, × 66.

Fig. 32. Pinnule sectioned in a plane paralleling the plane of the lamina. The midrib (*a*) is seen departing from the penultimate midrib (*b*). To the right of the pinnule midrib, several lateral veins are shown; to the left, five synangia are shown in transverse section. Slide #1706, × 20.

Fig. 33. Longitudinal section of a synangium, showing the pedicellate attachment to the lamina. Slide #1708, × 80.



MAMAY—FERN FRUCTIFICATIONS

Explanation of Plate

PLATE 7

Scolecopteris incisifolia

Fig. 34. Portion of a pinnule sectioned in a plane parallel to the midrib and at right angles to the plane of the lamina (this approximates the section shown in diagram *C*, text-fig. 1). The lamina proper is shown at the upper portion of the figure (*a*); below this are shown four synangia, transversely sectioned (*b*); below the synangia are several of the inflexed lobes of the pinnule margin (*c*). Slide #1709, × 45.

Fig. 35. Two immature synangia, longitudinally sectioned. Note the vascularized pedicels (*a*). Slide #1709, × 55.

Fig. 36. Transverse section of a lobe of the pinnule margin. Slide #1709, × 100.

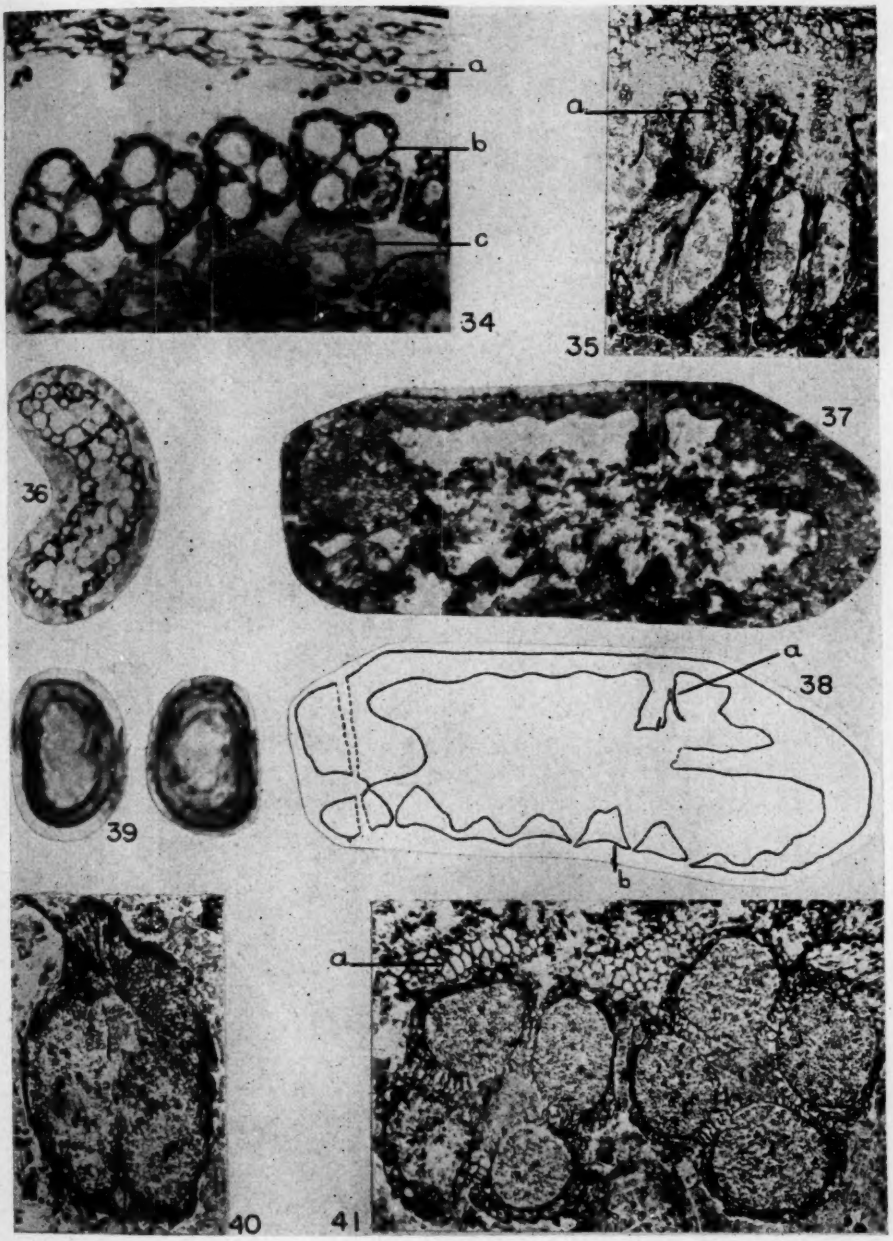
Fig. 37. Pinnule sectioned in a plane parallel to that of the lamina. (For clarification see fig. 38.) Slide #1712, × 18.

Fig. 38. Line drawing of the pinnule section shown in fig. 37. A portion of the midrib is shown at the right. The inflexed pinnule margin at the upper portion of the drawing is shown as a continuous tissue, with portion of a synangium attached (*a*). The opposite margin has been sectioned in a slightly lower plane, and is seen to be dissected. A marginal lobe is shown at point *b*.

Fig. 39. Spores. Note the thick spore walls. Slide #1711, × 1000.

Fig. 40. Longitudinal section of a synangium. Slide #1711, × 75.

Fig. 41. Transverse section of two synangia, each containing four sporangia. *a*, inflexed lobe of pinnule margin. Slide #1711, × 55.



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Explanation of Plate

PLATE 8

Scolecopteris major

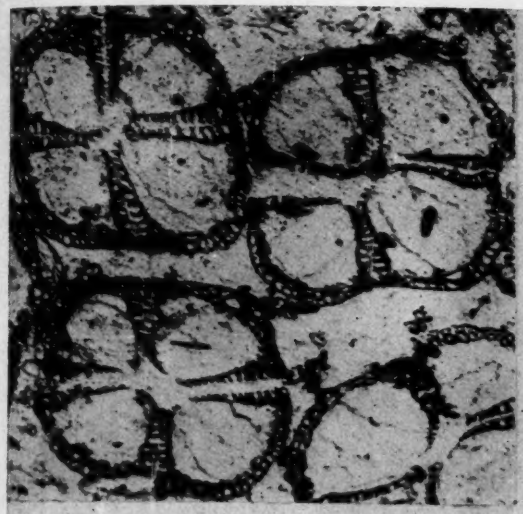
Fig. 42. Transversely sectioned synangia, each containing four sporangia. Note the thick outer walls of the sporangia and the slits of dehiscence along the innermost surfaces of the sporangia. Slide #1717, × 50.

Fig. 43. Longitudinal-transverse section of a synangium. The two sporangia in the upper portion of the figure are shown in transverse section; the two remaining sporangia are shown in a three-dimensional (longitudinal-transverse) view. Slide #1717, × 50.

Fig. 44. Longitudinal section of a synangium. Note the short, thick pedicel. Slide #1714, × 36.

Fig. 45. Spores. Note the thick triradiate ridge. Slide #1713, × 450.

Fig. 46. Apex of a sporangium, showing two multicellular hairs attached. Slide #1715, × 100.



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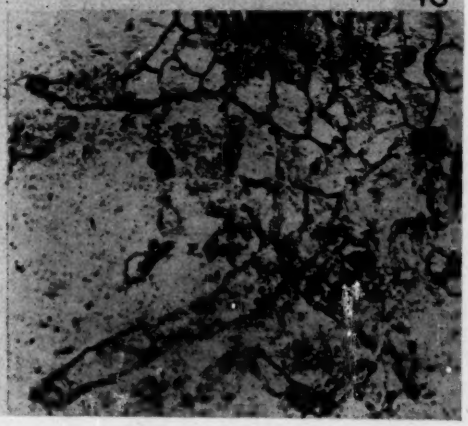

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EXPLANATION OF PLATE

PLATE 9

Eoangiopteris Andrewsii

Fig. 47. A pinnule sectioned in a plane parallel to that of the lamina, and slightly below it. The midrib (*a*) and several synangia are shown. Slide #1723, × 20.

Fig. 48. Two synangia. *a*, inflexed pinnule margin; *b*, receptacle of synangium. (For clarification of this section see text-fig. 2, D, which approximates the section shown in fig. 48, represents a section cut through plane *b-b'* of diagram B.) Slide #1720, × 54.

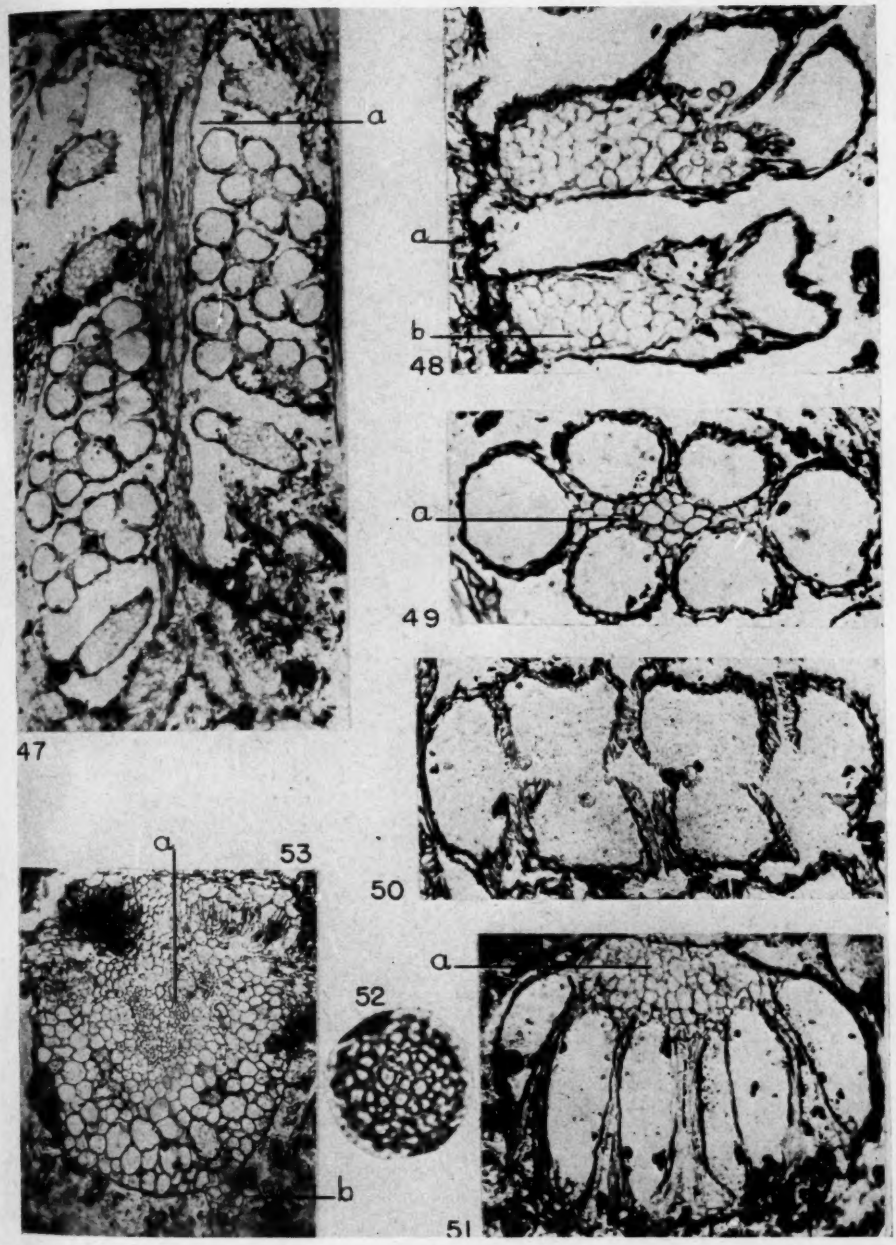
Fig. 49. Transverse section of a synangium. *a*, receptacle. (For clarification of this and fig. 50, see text-fig. 2, C, which represents a section taken through plane *a-a'* of B. The receptacle is stippled.) Slide # 1723, × 52.

Fig. 50. Transverse section of a synangium, taken in a plane above the receptacle. Note the slits of dehiscence along the innermost surfaces of the sporangia. Slide #1719, × 53.

Fig. 51. Longitudinal section of synangium. *a*, receptacle. Slide #1722, × 40.

Fig. 52. Spore. Note the reticulate exine. Slide #1719, × 370.

Fig. 53. Transverse section of a pinnule midrib. *a*, u-shaped vascular bundle; *b*, multicellular hair. Slide #1726, × 50.



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